The characteristic fauna
of inland drift sands

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Inland drift sands are a very harsh environment to live in because of an extreme microclimate, limited amount of nutrients and aeolian dynamics. Only a few animal species are able to cope with these conditions as a result of physical, physiological and behavioural adaptations, which makes drift sands relatively poor in species diversity. However, since drift sands are only available to adapted species, fauna composition is very characteristic and contains many rare and often threatened species. This chapter first describes the characteristic fauna of drift sands and the adaptations necessary for living in these 'Atlantic deserts'. The second part of the chapter discusses threats to characteristic species as well as thresholds for restoration and management of drift sand in relation to fauna.

An overview of the fauna of inland drift sands

Data on fauna of drift sands

Historic data on fauna of drift sands are scarce compared to other landscape types, such as heathland and coastal dunes; more dynamic pioneer stages therein have been especially neglected for a long time. In contrast to research on vegetation, studies on fauna had an almost anecdotal character for many decades and only since the 1980's more or less standardised methods were used to study and monitor faunal communities. Most of the data on fauna of drift sands which are discussed in this chapter are derived from Dutch studies and surveys reviewed in Bakker *et al.* (2003) and an ample research program on Dutch drift-sand ecosystems in the period 2006-2009 (Nijssen *et al.* 2010). Data on drift-sand fauna from other countries are rare, though larger studies exist for Belgium (Dekoninck *et al.* 2000) and Germany (Anders 2004). The Belgium study did not focus on active drift sand, but on stabilised 'land dunes' or 'moss-dunes', which are remnant sites of once larger scaled drift-sand areas. Almost all German sites and several Dutch and Belgium sites are (former) military training areas with gradients from open sand to dry heathland (in Germany called 'Offenland') of which large parts are – or resemble – drift-sand habitat (photo 14.1). These military areas often have a drift-sand origin. However, in Germany large parts were created by extensive military use of Holocene and Pleistocene substrates in the second half of the 20th century and do not have a history of aeolian activity (Beutler 2000). However, these recently created 'drift sand' habitats turn out to be important areas for typical animal species of 'natural' drift sands (Anders 2004).

Characteristics of drift-sand fauna communities

The majority of animal species in inland drift sands belong to the families of digging wasps and spider wasps (Hymenoptera, Sphecidae and Pompilidae), ants (Hymenoptera, Formicidae), beetles (Coleoptera; especially ground beetles Carabidae), and to a lesser extent flies (Diptera; especially robber flies Asilidae and stilleto flies

Photo 14.1 Former military areas like Jüterbog (Brandenburg, Germany) may not always have an aeolian history, but are inhabited by a large number of characteristic animal species of drift sands, like the tree grayling (*Hipparchia statilinus*), tawny pipit (*Anthus campestris*) and great grey shrike (*Lanius excubitor*) (photo Marijn Nijssen).

Therevidae) and spiders (Aranea). Other orders and families found frequently in drift sands are a.o. grasshoppers and crickets (Orthoptera), bees (Hymenoptera, Apoidae) and butterflies (Lepidoptera), but these groups are represented by fewer species. Insufficient data are available on several species rich invertebrate groups, such as parasitic wasps (Hymenoptera, Parasitica), spiders (Aranea) and rove beetles (Coleoptera, Staphylinidae).

Vertebrate species are scare in drift sands, with only a small number of bird species belonging to the characteristic fauna. Some mammals (for instance roe deer *Capreolus capreolus*), reptiles and amphibians (like smooth snake *Coronella austriaca*, natterjack toad *Bufo calamites*, and common spadefoot *Pelobatus fuscus*) use drift sands for foraging or, for reptiles and amphibians, digging in bare sand to hide or hibernate. However, they rely mainly on adjacent habitat types to fulfill their life-cycle (Bakker *et al.* 2003). The main reason for the lack of vertebrates is probably a very low availability of calcium in the system. Due to low production rates of biomass, detritivores such as millipedes (Diplopoda), woodlice (Isopoda) (Dekonick *et al.*, 2000) and earthworms (Oligochaeta, Lumbricidae) (Nijssen *et al*, 2010) are low in abundance as well as in species diversity and only appear in later stages of vegetation succession when organic soil and litter layers are formed (see also chapter 9).

Table 14.1 Trend and status of characteristic animal species of Dutch drift sands and their association to drift-sand areas in the Netherlands (defined as % of occupied square kilometres overlap with drift sand) in the period after 1980, before 1980 and shifts in association between these periods (after Nijssen *et al.* 2010; analyses by EIS-Netherlands, SOVON Dutch Centre for Field Ornithology and Dutch Butterfly Conservation). Analysis for breeding bird association was for 1978-2009. Only species which have more than 25% association with drift sands and a minimum of 5 records within drift sands are shown. N = new (only found after 1980). Trend (since 1980): -- = strong decrease, - = decrease, ± = stable, + = increase, ++ = strong increase. Status: VR = very rare; R = rare, S = scarce, C = common. Red List: CE = critically endangered; E = endangered; V = vulnerable. Notes: * No official Red List available, status after Peeters *et al.* 2004; ** Species decreased since publication of the Red List and should be considered as CE now. *** Species extinct after publication of the Red List; T = species nests in trees and is probably associated with forest on poor sandy soils.

		association after 1980 (%)	associtaion before 1980 (%)	shift in association	trend in NL	status in NL	Red List Status (NL)
Wasps and bees							
Eoferreola rhombica	Ladybird spider-wasp	80	.	N	.	VR	.
Hedychridium femoratum	cuckoo wasp	75	.	N	+	VR	.
Tachysphex helveticus	grasshopper-wasp	60	11	5	-	VR	.
Cryptocheilus notatus	spider-wasp	36	8	4,5	-	R	.
Omalus biaccinctus T	cuckoo wasp	29	12	2,3	±	S	.
Priocnemis pusilla	spider-wasp	29	7	3,5	±	R	.
Pemphredon lugens T	aphid-wasp	27	.	N	+	S	.
Miscophus spurius	dwarf spider wasp	27	17	1,8	--	VR	E*
Lasioglossum quadrinotatum	sweat bee	27	2	N	--	VR	E*
Pemphredon austriaca T	aphid-wasp	9	50	0,2	+	S	.
Ants							
Strongylognathus testaceus	-	52	17	2,5	--	R	.
Formica rufibarbis/ lusatica	-	41	.	N	±	C	.
Tapinoma ambiguum	-	36	-	N	--	VR	.
Myrmica lonae	-	30	50	0,4	.	.	.
Formica pratensis	-	28	17	1,5	±	C	.
Solenopsis fugax	-	26	5	3	±	S	.
Other invertebrates							
Hipparchia statilinus	Tree grayling	64	35	1,8	--	VR	E**
Labidura riparia	Tawny earwig	56	17	6,3	.	S	.
Eresus sandalianus	Ladybird spider	50	33	1,6	.	R	.
Boreus hyemalis	Snow scorpionfly	38	14	6,5	.	S	.
Ectobius pallidus	Spotted mediterranean cockroach	36	.	N	.	.	.
Stenobothrus lineatus	Stripe-winged grasshopper	28	2	21,2	-	R	V
Ephippiger ephippiger	Sadle-backed bush cricket	27	9	4,5	--	R	E
Gryllus campestris	Field cricket	26	13	4,5	--	R	E
Birds							
Anthus campestris	Tawny pipit	92	.	.	--	VR	CE***
Lanius excubitor	Great grey shrike	69	.	.	--	VR	CE***
Caprimulgus europaeus	Eurasian nightjar	29	.	.	.	R	V
Jynx torquilla	Eurasian wryneck	29	.	.	--	VR	CE
Lulula arborea	Tree lark	26	.	.	.	C	.

Characteristic animal species of drift sands

The drift-sand landscape consists of a gradient from bare sand dunes to dry heath and open forest. It is obvious that the faunal communities of drift sands overlap with those of similar landscape types such as coastal dunes, riparian dunes and dry heathland (Bakker *et al.* 2003). In order to determine the association of animal species with drift sand, an analysis was made for a selection of Dutch fauna, for which ample distribution data exist in a standardized scheme based on presence in square kilometers. This selection consisted of around 3700 species, including breeding birds, wasps, ants, bees, butterflies, hover flies (Diptera, Syrphidae), ground beetles and several smaller taxonomic groups (Nijssen *et al.* 2010). A total of 162 animal species (4.4% of the analyzed species) are associated with inland drift sand, which means that at least 20% of their population is located within drift-sand areas (a shortlist is presented in table 14.1). Therefore, a few percent of Dutch biodiversity is to be maintained by vital inland drift sands. For several invertebrate groups, a high percentage of species is associated with drift sands, such as ants (23.6%), ground beetles (12.5%) and wasps (5.9%), which emphasizes the importance of drift sands as a habitat for these groups. Not all species associated with drift sands are living in open biotopes. Approximately 15%, mainly wasp and hover fly species, live in (or on edges of) dry forest, which cover large areas of historic drift-sand areas. Although it is disputable whether these species should be classified as characteristic for drift sands, they are strongly associated with the drift-sand landscape in a broader sense.

Based on the analyses of animal species association with drift sands (as described above), it turns out that there are no strict drift-sand specialists; not a single species occurs only in drift sands for a period of several decades. Although true drift-sand specialists do not exist, several species are strongly associated and can be seen as characteristic drift-sand species. The strongest association is found for tawny pipit

Photo 14.2 Tree grayling (*Hipparchia statilinus*) in its natural habitat of NW-Europe. It is one of only a few butterfly species which live in these 'Atlantic deserts' (photo Marijn Nijssen).

Photo 14.3 Caterpillar of the tree grayling (*Hipparchia statilinus*) on grey hair-grass (*Corynephorus canescens*) just after moulting from the 2nd to 3rd larval instar, indicated by the old skin fragments on the abdomen and a relatively large head.

Anthus campestris (92%), ladybird spider-wasp *Eoferreola rhombica* (Hymenoptera, Pompilidae) (80%), the cuckoo wasp *Hedychridium femoratum* (Hymenoptera, Chrysididae) (75%), great grey shrike *Lanius excubitor* (69%) and tree grayling *Hipparchia statilinus* (64%) (photos 14.2 and 14.3).

Sufficient data were available for 53 species to analyze shifts in association with drift sands between the periods before and after 1980. After correction for differences in research intensity between these periods, it turned out that the association of characteristic drift-sand species has become stronger in the past decades, which could also be concluded for several mushroom, liverwort and lichen species (see chapters 10, 12 and 13). Of all analysed species, association with drift sand increased for 29 species (55%), while it decreased for only 9 species (17%). A total of 15 species (28%) was only present after 1980. An increase in association with drift sands is also found in precise descriptions of population trends of species presently seen as typical for inland drift sands: tree grayling, tawny pipit, great grey shrike, Eurasian wryneck *Jynx torquilla*, as well as inland populations of northern wheatear *Oenanthe oenanthe* (SOVON 2002, Van Turnhout 2005, Bos *et al.* 2006). All of these species occurred in earlier days in many kinds of dry open landscapes in the Netherlands, such as dry heathland, extensive dry arable land and river dunes. Since total area as well as quality of these landscapes decreased dramatically during the last century, all species vanished in these biotopes and became more and more restricted to drift sands. These species are nowadays seen as drift-sand specialists, but in fact only became specialists because other landscapes were lost or became unsuitable. Drift sands thus function as a refuge, which makes conservation and restoration even more important, though it might well be that this habitat is in fact suboptimal for some of these species. Restoration of degenerated sandy biotopes outside drift sands will, in that case, be necessary for durable conservation of the populations.

Status and trends of drift-sand fauna

Many animal species of drift sands and similar habitat types are really bound to these habitats. Since drift sands as well as other dry, sandy habitats declined rapidly in size, number and quality during the last century, it is not surprising that many of these species are (nowadays) rare and assigned to the Red List, or have recently gone extinct. Examples of these species are tree grayling (extinct in Belgium, 1 population left in the Netherlands, vulnerable in Germany), tawny pipit (extinct in Belgium and the Netherlands, critically endangered in Germany), Eurasian wryneck (critically endangered in Belgium and the Netherlands, endangered in Germany) and great grey shrike (extinct in the Netherlands, critically endangerd in Belgium and Germany) (Bauer *et al.* 2002, Hustings *et al* 2004, Devos *et al.* 2004). In their large scale study on Belgium drift-sand remnants, Dekoninck *et al.* (2000) mentioned that 37 species (19,6%) of spiders, 24 species (24%) of ground beetles and 3 species (25%) of grasshoppers are on the Red List. Most Red List-species were found in pioneer

vegetation and nutrient-poor grasslands, rather than in adjacent dry heathland or open forest. Nijssen *et al.* (2010) found similar results for the Netherlands. The majority of species associated with drift-sand areas is scarce (less than 10 records since 1980) and at least 36% of these species are (strongly) declining. Of all characteristic drift-sand species of birds (8), butterflies (1), bees (2) and grasshoppers (4), up to 86% are stated on a Red List in the Netherlands. No Red Lists are available for other faunal groups. Based on the data presented above, it is clear that drift sands play a significant role in the maintenance of faunal diversity in North-western Europe.

Traits and tactics in fauna of drift sands

Coping with adverse conditions in drift sands

Drift sands are a very harsh environment to live in. Starting with only bare sand, nutrient levels are very low and the microclimate is extreme. These conditions hamper biomass production, which keeps the amount of organic matter and food sources for herbivores and detritivores low throughout decades of vegetation succession (see chapters 7 and 11). In addition, aeolian dynamics of bare sand causes physical stress as well as sudden changes in landscape composition, which makes the dynamic parts of drift sands an unpredictable biotope for animal species. These challenging conditions can only be coped with by specialised species which have physical, physiological and behavioural adaptations. Drift sands are therefore relatively poor in species diversity and abundance. The advantages of these harsh conditions are a copious amount of solar heat, which is necessary for many invertebrate species to develop, a low degree of competition for food sources, low predation pressure and a minimal chance of fungal and bacterial infections. In the next part of this chapter, important traits for drift-sand species are described (after Stearns 1992, Chapman 1998, and Begon *et al.* 2006 unless referred otherwise).

Extreme microclimate

Animal species living in drift sand and other warm and dry biotopes are often called 'thermophilic' or 'xerophilic'. These words literally mean 'liking' warmth or drought, but this qualification is ecologically incorrect. All animal species depend on a certain amount of warmth for their development from egg to adult stage, though 'thermophilic' species depend on higher threshold temperatures to start development and/or need a larger total temperature sum to complete their life cycle. Optimum temperature for development might be higher than in generalist species, though high temperatures can be dangerous as protein structures are harmed. These species can only reproduce in warm biotopes, thus, in Europe, many of these species have a southern distribution range. Towards the northern borders of their range

they can only establish populations in very open biotopes (like drift sands, coastal dunes and dry heathland) where solar heat is not hampered by a dense high vegetation or thick litter layer. In these northern areas, population size often fluctuates strongly depending on year to year differences in weather conditions. Subsequently year to year differences in chances of local extinction of (smaller) populations or colonization of unoccupied areas occur.

Species referred to as 'xerophilic' are resistant against desiccation and therefore (to a certain level) insensible for dry conditions. These species do not directly depend on dry conditions for survival or development, though the fact that many parasites (like bacteria and fungi) cannot flourish under dry conditions significantly increases survival of drought resistant species. Most drought resistant species occur in steppe-like biotopes in Eastern and Central Europe where the continental macroclimate can cause long periods of desiccation in summer as well as dry winters.

Resistance to drought and overheating can be obtained through various adaptations. First, many species escape the most warm and dry periods by synchronizing their activity to periods with moderate climatic conditions. The majority of drift-sand species live nocturnally, hiding at daytime in the soil or in the shelter of plants and dead branches. Shade of solitary trees, forest edges and other high vegetation structures are mentioned as being important – or even crucial – for thermoregulation of characteristic day active butterfly species such as the tree grayling and grayling *Hipparchia semele* (Bos *et al.* 2006, Shreeve 1990).

The reproductive period is often in autumn, winter or early spring, thereby escaping the most extreme climatic conditions of summer. Some species of soil macrofauna, such as larvae of the snow scorpion fly *Boreus hyemalis* (Raemakers & Kleukers 1999) migrate to deeper soil layers up to 30 centimeters depth, where temperature as well as humidty are moderate. In a pilot study in several Dutch drift sands, it turned out that 11 to 23% of all soil micro arthropod individuals lived at more than 5 centimeter depth, while in forests and agricultural grassland this percentage does not transcend 3% (Nijssen *et al.* 2010). Many species can make use of delayed development at different moments in their life cycle (from egg to reproducing adult) to overcome periods of adverse climatic conditions in winter (hibernation) as well as in summer (aestivation). Two mechanisms can be distinguished; a facultative delay of development which is triggered directly by adverse conditions, such as low temperatures (quiescesence), and an obligate delay of development (diapause), which evolved in response to regularly recurring periods of adverse conditions and is triggered by seasonal indicators such as photoperiod and threshold temperature levels.

The few diurnal species which are active in open areas during summer have several physical adaptations to diminish the effects of heat and drought. Many diurnal ground beetles and tiger beetles (Coleoptera, Carabidae and Cicindelinae*)* have metallic coloration on elytra, pronotum, head and sternites for reflection of solar radiation. Tiger beetles as well as characteristic spiders of dry habitats often possess

long hairs or bristles to minimize evaporation (Almquist 1971) (photo 14.4). Although larger species (or individuals) are better able to keep homeostasis under severe conditions, Almquist (1971) found no correlation between the size of the species and their tolerance to low humidity, which stresses the importance of behavioral, physical or physiological adaptations to withstand adverse conditions in drift sands.

Aeolian dynamics

Aeolian dynamics created drift sand and inextricably belong to the drift-sand landscape. Bare sand which is moved by the wind is the most extreme environment of drift sands, and is hardly liveable for animals. Although some individuals may be found on bare sand (mostly mobile species exploring the area), true colonization of pioneer habitats by animal species starts only after grey hair-grass *Corynephorus canescens* or haircap-moss *Polytrichum piliferum* have more or less stabilised sand movement and food resources (vegetation biomass) begin to grow. Also in these

Photo 14.4 The tiger beetle *Cicindela hybrida* is one of the few diurnal predators in pioneer stages of drift sands, being protected against heat and drought by metallic coloration, mainly on legs and underparts, and long white hairs (photo Marijn Nijssen).

early succession stages, aeolian dynamics cause accumulation as well as deflation of sandy substrate, which makes this biotope highly unpredictable. Contemporaneously, burial by sand forces grasses and mosses to grow which leads to a relative high production rate of vital root and shoot biomass. To use these productive, but unpredictable, habitats animals should be able to escape periods with high aeolian activity in time (synchronisation of life cycle) or space (mobility). Reproductive periods of animal species living in pioneer habitats are mainly in spring when aeolian activity is generally low and the amount of food is high. Simultaneously, the percentage of mobile species (macroptere species with flight capability) is very high compared to stable biotopes. Mobility is often seen as an adaptation to escape adverse condition and colonize new suitable areas (a.o. Den Boer 1990). Another way of escaping the dynamic surface is digging, a property which is widespread in pioneer species of active drift sands, such as the tawny earwig (*Labidura riparia*; Dermaptera, Labiduridae), larvae of root-eating scarabid beetles (Coleoptera, *Scarabaeidae*) and larvae and adults of the ground beetle genera *Harpalus* and *Amara* (see chapter 9).

Low nutrient availability

Nutrient levels are very low in bare sand and, because adverse microclimatic conditions hamper biomass production, the amount of organic matter and thus of primary food sources remains low for decades. This low nutrient status of drift sands is one of the main reasons for the low number and limited abundance of animal species. Elton (1927) already noticed that, since energy is lost with each step within a food chain, the energy base of a community determines the total length of the food chain found in it. A small energy base therefore supports fewer steps, which limits the number of possible niches and the mean abundance of species. The precondition of low nutrient level leads to two other mechanisms which drive animal diversity and are described for deserts and other drylands by Ayal *et al. (*2005). First, low food quality of plant tissues (living and dead) in combination with low microbiological activity due to the extreme microclimate lead to relatively large primary consumers in herbivores and macro-detritivores (like *Tenebrionidae* and *Scarabeidae* beetles). Since predators are generally much larger than their prey, a food web based on large primary consumers will support fewer steps than a food web based on small primary consumers. Second, low food quality will benefit species that are energetically efficient, which means that drift sands are in general more suitable to small poikilotherm species than to larger homoeotherm species like birds and mammals. Plants living in dry and poor environments often grow slowly and invest in conservation or efficient re-use of nutrients; growth and reproduction are limited to a short period in the most moderate part of the season (stress-tolerators in Grime's triangle (1977)). In drift sands, these species are represented by winter annuals, such as barestem teesdalia (*Teesdalia nudicaulis*) and Morison's spurry (*Spergula morisonii).* This means that primary food sources of higher quality are scarce in drift sands

and limited to a short period in late autumn (when most seeds germinate and seedlings are present) and early spring. Primary food sources which are present throughout the year consist of seeds (often protected by a thick cuticulum), litter, detritus and less nutritious or less digestible roots and shoots. Since nutrients are difficult to extract from most plants, almost all herbivores living in drift sands have to develop slowly. Combined with obligate diapause or facultative dormancy to survive adverse climatic conditions and to synchronise foraging period with presence of suitable food, most herbivores can only have annual or even biennial generations. Examples are the butterfly species tree grayling, grayling and silver-spotted skipper *Hesperia comma*, of which the caterpillars live on small-leafed grass species like grey hair-grass and *Festuca* species (Bink 1998). A particular good example of slow development in herbivores is the snow scorpion fly, of which the larvae feed on low nutritious rhizomes of mosses and development takes two years to reach the adult stage of only several millimetres in size (Raemakers & Kleukers 1999).

Flowering plants are scarce in drift sands, which limit food sources for nectar and pollen feeding taxa like bees, flies and butterflies. Large bee species, for instance *Andrena* species (Hymenoptera, Andrenidae) and *Dasypoda hirtipes* (Hymenoptera, Dasypodaidae), can nest in open drift-sand biotopes, but forage up to a few kilometres from their nest on flowering willow species (*Salix* sp.) and yellow composites. Smaller *Andrena* species, with a limited radius of action, can live only in drift sands where creeping willow *Salix repens* grows close to nesting sites. In late summer, common heather *Calluna vulgaris* is an important food source, for instance for monotrophic bee species *Colletes succinctus* (Hymenoptera, Colletidae) and *Andrena fuscipes* as well as the butterfly species grayling and tree grayling.

Strictly predatory species are not very common in drift sands, especially not in pioneer stages where biomass is low and subsequently the abundance of primary consumers and detritivores – which are potential prey for predators – are low. This is illustrated by the high number of herbivore – or better granivore – ground beetles living in grey hair-grass vegetation. Ground beetles originally are carnivorous and evolution to herbivory within this group is seen as a relatively rare exception to the rule. In grey hair-grass, the percentage of herbivore species can however be 40%, while the percentage of herbivorous individuals can rise to over 80% (Nijssen *et al.* 2010).

Parental care by feeding offspring is a rare trait among invertebrate species, but can be very profitable to enhance offspring survival when food resources are scarce. In drift sands, parental care is present in several non-related invertebrate species, such as the tawny earwig, ladybird-spider *Eresus sandaliatus* and digger wasp *Ammophila pubescens* (Hymenoptera, Sphecidae). Females of the tawny earwig, as well as *Eresus sandaliatus*, feed first instar juveniles while they live inside a burrow, protecting their offspring in their most vulnerable life stage against predators as well as adverse climatic conditions **(lit)**. Females of *A. pubescens* provision their offspring with paralysed lepidopteran caterpillars, but, unlike most other digger

wasps, each offspring is fed gradually as it grows. Starting with one caterpillar on the first day, the nesting burrow is closed with a small stone and controlled after several days. After the egg is hatched and the larvae is feeding on the first caterpillar, the female provides the nest with another 7 to 9 caterpillars within a few days, before permanently closing the burrow, leaving the larvae to pupate (Baerends 1941).

Parasitoidy is a feeding guild which is relatively abundant in drift sands. The advantage for parasitoids in a nutrient poor environment is that they obtain their nutrients from one or more host individuals, but – in contrast to predator-prey relationships – they are generally smaller than their host species. A constraint for abundance however is that host species population should be abundant enough. For instance, large spider wasps, which live on large spiders, seem therefore restricted to larger drift-sand areas where sufficient population of hosts are available. Parasitoids and parasites are especially numerous in wasps, bees and ants (Hymenoptera, *Aculeata*), ranging from social parasitism by ants (using 'slave' workers of another species to rear their progeny) to brood parasites of the first and second order (hyperparasites). For almost every invertebrate group within drift sands, at least one, but often more specialized parasitic hymenoptera species, are present. Most prominent are several digger wasp species of the genus *Tachysphex* (Hymenoptera, Crabronidae); parasitoids on grasshoppers, cockroaches and several other invertebrate groups and spider wasps Hymenoptera, Pompilidae). Of this last group, almost 50% of all Dutch species find their optimum habitat in drift sands and coastal dunes (Peeters *et al.,* 2004). Hyperparasites occur in spider wasps, such as the cuckoo spider wasp *Ceropales maculata* parasitizing on the grey spider wasp *Pompilus cinereus*, which in turn parasitizes mainly on wolf spiders (*Lycosidae*). An extraordinary species is the spider wasp *Eoferreola rhombica*, which is a parasite on the ladybird spider *Eresus sandaliatus* Although the species most probably belongs to the indigenous fauna of the Netherlands, it was only discovered no earlier than 1998 (Raemaeckers & Van Helsdingen, 1999) and until now only a few records are known, almost solely from drift sands. The closest populations are situated in Northern France and Eastern Germany, approximately 500 kilometres away from the Dutch population. The Dutch population of *Eofereolus rhombica* seems unique for it is probably the only one in the world linked to the ladybird spider species *Eresus sandaliatus* as a host.

A food source which is often neglected, but can be of significant importance in poor ecosystems, is the sugar-rich secretion of aphids and other insects (mainly *Homoptera*) known as 'honeydew'. Many wasp and ant species use honeydew as a source of energy necessary to reproduce and collect food for their offspring. Especially aphids feeding on deciduous trees (in drift sands mainly oak *Quercus sp*, birch *Betula sp*. and alder buckthorn *Frangula alnus*) produce large amounts of honeydew and can be very important energy sources in nutrient poor drift sands for a wide variety of wasps and ant species.

From traits to tactics

To understand how animal species are able to live in drift sands, it is necessary to understand the differentl adaptations or traits which they have developed, as well as the combination of traits forming life-history tactics, defined by Stearns (1976) as "a set of co-adapted traits designed, by natural selection, to solve particular environmental problems: a complex adaptation". However, although the idea of using traits and life-history tactics for analyzing animal communities has existed for many decades, data on species traits is scarce and only for very few species groups have life-history tactics been unraveled – for instance soil micro-arthropods (Siepel 1994) and several groups of aquatic invertebrates (Verberk *et al.* 2008).

First attempts for using life-history tactics for drift-sand species were made by Siepel & Nijssen (chapter 9 of this book) for soil micro arthropods and by Nijssen *et al.* (2010) for understanding distribution ranges of characteristic ground beetle species within drift sands. In figure 14.1, ground beetle species distribution is shown over a vegetation succession gradient from pioneer grey hair-grass vegetation, via haircap-moss to stable lichen rich open grasslands or vegetation dominated by the invasive moss species *Campylopus introflexus*. Pioneer habitat is inhibited by very mobile diurnal carnivores – mainly the tiger beetle *Cicindela hybrida* hunting by sight – and nocturnal herbivores of the genera *Harpalus* and *Amara*. Nocturnal carnivores are (compared to other stages) scarce, since these species need a large number of prey when foraging by touch in the dark. When vegetation succession continues and biotopes become more stable, flightless species increase in abundance, probably being more competitive than flying species since they do not have to spend energy on the development of wings and flight muscles. At the same time, the main reproductive period shifts partly from autumn to spring, since conditions for offspring (food abundance, microclimate and predictability) are much better than in pioneer stages. Note that several combinations, like being a flying diurnal carnivore
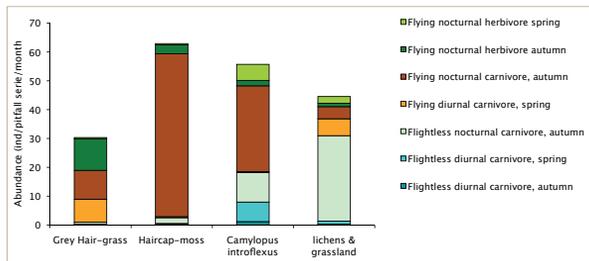

FIG. 14.1 **Mean abundance of ground beetle species divided into 7 life-history tactics in a succession range from pioneer grey hair-grass vegetation to 50 year old lichen rich open grasslands (after Nijssen *et al.* 2010).**

reproducing in autumn, do not occur in drift sands. This example shows that even simple analyses of traits and tactics can create clear insights to mechanisms driving the distribution patterns of species.

Threats for fauna of drift sands

Many characteristic animal species of drift sands have declined dramatically over the last century and some are already extinct. A very important reason for this deterioration of drift-sand communities is without doubt the enormous decrease of open drift-sand area (for the Netherlands from 80.000 to 1400 hectares within 150 years) and the subsequent fragmentation of drift-sand sites. These drift-sand sites now function as a refuge for rare and threatened animal species, even more so since other dry, open landscape types, like river dunes, dry arable land and dry heathland, disappeared or became unsuitable. However, characteristic animal species declined or have become extinct also in large and apparently suitable drift-sand areas. The ample research program on Dutch drift-sand ecosystems from 2006-2009 (Nijssen *et al.* 2010) tried to get a grip on current major threats for animal species in drift sands.

Looking at the basic ecological mechanisms for faunal diversity in drift sands, it will not be a surprise that the main problems causing decline of animal species are those which mitigate the extreme conditions of these 'Atlantic deserts'. Characteristic species of drift sands are, in contrast to generalist species and infectious organisms, adapted to survive under adverse conditions such as drought, heat and low nutrient levels. The price they pay for being adapted is that they are not very competitive or are vulnerable to diseases and parasites in certain stages of their life cycle. At the moment when the extreme, adverse conditions in drift sands are mitigated, the characteristic species will be out-competed by generalist species or mortality can increase due to bacterial and fungal infections. The two most important factors mitigating conditions in drift sand are (former) stabilization of active drift sands and increased airborne nitrogen deposition. Direct and indirect effects of these factors on drift-sand ecosystems are: (1) decreased area and subsequent fragmentation of drift-sand areas, (2) early stabilization of open sand and faster vegetation succession, leading to (3) changes in distribution of vegetation succession stages within drift sands and (4) development of dense organic layers, (5) changes in food quality of plants, (6) mitigation of extreme microclimatic conditions and (7) decreased prey availability for insectivorous bird species due to cumulative negative effects on the abundance and diversity of invertebrate species.

The effects of decreasing total drift-sand area and fragmentation of remnant sites, such as an increased chance of local population extinction and inbreeding or decreased (re)colonization possibilities, have never been studied for drift sands, but will definitely play major roles, as they do in many landscape types (a.o. Settele *et*

Saunders *et al*. 1991). Invertebrate species diversity of 7 drift-sand areas in the Netherlands, differing in size, isolation and biotope composition, differed only slightly and was mainly correlated with area size and biotope composition within the areas (Nijssen *et al*. 2010). This indicates that loss of total area and quality of drift-sand habitat probably outweigh the effects of habitat fragmentation (conform Fahrig 1997).

A strong increase in recreation pressure (and sometimes military activities) on drift sands is sometimes mentioned as a problem for faunal communities, especially for ground breeding bird species which are sensitive to disturbance. Negative effects of human disturbance are proven for the Eurasian nightjar in England (Liley & Clarck 2003), the northern wheatear in the Netherlands (Van Turnhout 2009) and are suggested for the tawny pipit by RG Bijlsma (1990 & 2002). The impact on invertebrate species is less clear. Negative effects of heavy trampling by humans on invertebrate species has never been studied in drift sands, but trampling by cattle in coastal dunes can have severe negative effects on insects nesting in the soil (Bonte & Maes 2008). However, in totally stabilized drift-sand sites, disturbance by humans and cattle is the only factor keeping bare sand open and might be the reason for survival of remnant populations of invertebrate species associated with bare sand, such as suggested for the tawny earwig in the Beerzerzand area in the Netherlands (Van den Ancker *et al*. 2004).

The effects of decreased aeolian dynamics, fast vegetation succession and soil development by active stabilization and increased nitrogen deposition are complex, with many positive feedback mechanisms present. Also, high nitrogen deposition benefits the invasive moss species *Campylopus introflexus*, which can only become dominant in areas with a total N-deposition over 30 kg/ha/yr (see chapters 8 and 13). This moss species can develop a dead organic layer of several centimeters within a few years, causing significant mitigation of microclimatic conditions just above the vegetation. Effects of these single and cumulative changes on fauna were studied by Nijssen *et al*. (2010). Although many mechanisms are far from clear, and some must still be regarded as hypotheses, several important problems for animal species seem to occur. The three most important ones are described below.

Mitigation of extreme microclimatic conditions

Extreme climatic conditions make drift sands a difficult landscape to live in. Most characteristic species of drift sands have colonised this biotope from other natural habitats where conditions are so extreme that plant growth is limited, such as steppe and dry Mediterranean grassland. Animal species are associated with these habitats because they need a certain amount of solar heat to develop (mainly species from southern Europe) or because they have to escape predators or parasites during a vulnerable stage in their life cycle (mainly steppe species from eastern and central Europe). For species from both groups, dry sandy biotopes like drift sands, dry heathland and coastal dunes are the only suitable habitat in NW-Europe. An

example of a southern representative is the tawny earwig. Development of this species from egg to adult can take place within 44 days, but this strongly depends on temperature levels (Tawfik *et al*. 1972). While the species has 2 full generations and a partial 3rd generation a year in southern Europe and Egypt, only 1 full generation each year is found in Dutch populations with a (partial) 2nd generation only in years with a high total temperature sum (Nijssen *et al*. 2010). The tree grayling is also a common species in southern Europe, but many northern populations have become extinct, for instance in Belgium, Northern France and large parts of the Netherlands (Bos *et al*. 2006). Differences between southern and northern populations in adult size and coloration – with northern individuals being smaller and darker – indicate adaptations to relatively cooler biotopes and, in combination with large gaps between the northern and southern populations, genetic divergence and even the existence of different (sub)species are suggested (Peet & Soerink, 2001; Bouwman *et al*. 2010). Only one population of tree grayling has survived in the Netherlands, living on the largest active drift sand in the central part of the country. The species hibernates as vulnerable first instar larvae and mortality in winter, therefore, seems the most important bottleneck for tree grayling populations. A comparison between microclimatic habitat conditions in winter of a vital population of tree grayling in Jüterbog, (Brandenburg, Germany; see picture 14.1) and the last Dutch population showed significant differences in air relative humidity (RH) at 2 centimetres above the soil, the average height on which larvae hibernate on grey hair-grass tussocks (Nijssen *et al*. 2010). Mean RH in haircap-moss vegetation was above 90% in both areas, but the number and frequency of dry periods (RH beneath 75%) differed significantly, with 2 or 3 periods of desiccation a week in Brandenburg and only 2 or 3 each month in the Netherlands. This difference is caused by the continental climate in Eastern Germany versus the Atlantic climate in the Netherlands, but stresses that conditions in 'Atlantic deserts' are moderate – and therefore less suitable – compared to the continental 'steppe-climate'. Dominance by dense carpets of the invasive moss *Campylopus introflexus*, caused by high nitrogen deposition in the Netherlands, further decreased desiccation frequency to only once a month. Analyses on population trends of tree grayling in the Netherlands over 15 years (1993-2009) showed that periods of desiccation (formulated as mean RH of the driest winter month in the period November to February) is indeed negatively correlated with the growth factor of the population (Fig. 14.2). Mean humidity of the driest month lower than approximately 75% is correlated with population growth, while mean humidity of the driest month higher than 75% is correlated with a decrease in population size. RH of the most humid month did not correlate with population trends. The most probable reason for this higher winter mortality are increased infection rates by fungi or bacteria.

It is hypothesised that increased mortality in winter due to a more humid microclimate is a major threat to drift-sand species of eastern 'steppe' origin (like northern populations of tree grayling), while lowering of the total temperature sum
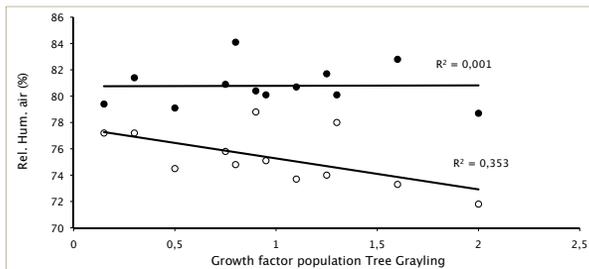
FIG. 14.2 Correlation between growth factor of the Dutch population of tree grayling (*Hipparchia statilinus*) and mean relative air humidity (RH) of the driest winter month (November – February) over the period 1993-2007. Data on population trend by Dutch Butterfly Conservation, data on air humidity by the Dutch Meteorological Institute KNMI (www.knmi.nl).

by encroachment of trees, dense grasses or organic soil layers will be a bottleneck for species of southern 'Mediterranean' origin (like the tawny earwig). It is obvious that global climate changes will affect population dynamics of drift-sand species, however differences in climate change scenarios, as well as numerous positive and negative feedback mechanisms between factors determining population trends, make prognoses on species level most uncertain.

Effect of increased nitrogen deposition on food quality of grey hair-grass

Since inland drift sands are very poor in nutrients it is expected that a high input of airborne nitrogen will have strong effects on the growth strategy and chemical composition of plants. The most important food plant in drift sands is grey hairgrass, which is present from pioneer vegetation to old stabilised grasslands. Only in active parts of drift sands is it buried by sand and growth is constantly stimulated. Food quality of host plants for herbivores is mainly determined by the amount of nitrogen available for uptake in relation to dry weight of the plant, which mainly consists of cellulose. Therefore, the C/N-ratio is often used as a simple measure for analysing food quality (Chapman 1998). When this is done for grey hair-grass in drift sands in a gradient from low (15 kg/ha/yr) to high N-deposition (50 kg/ha/yr), N% of the plant is positively correlated with N-deposition (Fig. 14.3). Since C% is similar between all sites (44%-46% of biomass), also the C/N ratio increases with higher N-deposition. This is thought to improve the food quality for herbivores (conform Troop & Lerdau 2004), but levels of amino acids in the same plants did not differ between sites. This suggests that the nitrogen surplus is stored in other, indigestible non-protein chemical compounds (NPN), which might lower food quality for

herbivores. This is supported by a 20% smaller size of the marbled grasshopper *Myrmeleotettix maculata*, which was sampled on sites where grey hair-grass had high levels of NPN (Fig. 14.4). Deposition of sand on grey hair-grass in dynamic sites increases total N percentage as well as the total amount of amino acids, thereby decreasing NPN in leafs (Fig. 14.3). Aeolian dynamics might therefore be a process diminishing the effects of high nitrogen deposition on food plant quality. It is far from clear which chemical compounds form NPN in plants or which mechanisms control the assembly of NPN instead of amino acids (Nijssen *et al.* 2010).
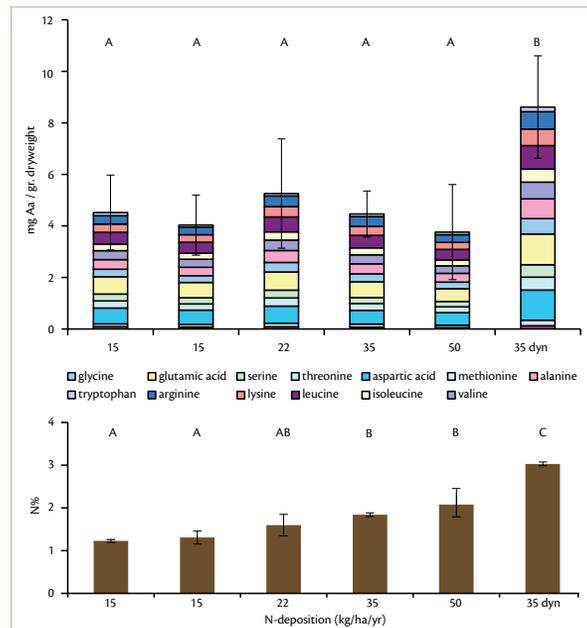

FIG. 14.3 (A) Total N% and (B) amount of amino-acids in grey hair-grass in drift-sand areas in a gradient from low to high nitrogen deposition. 35 dyn = plant samples taken in a dynamic site where grey hair-grass is regularly buried by sand and a N-deposition of 35 kg/ha/year. One-way ANOVA with Tukey Post-hoc test.
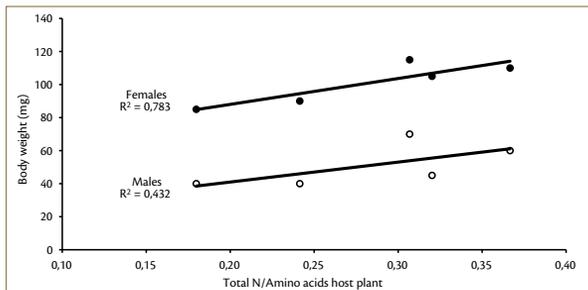
FIG. 14.4 Correlation between body weight (mg) of the marbled grasshopper *Myrmeleotettix maculata* and food quality of grey hair-grass (expressed as the ratio of total N and amount of amino acids), sampled at 5 different drift-sand areas in a gradient of N-deposition of (f.l.t.r.) 15, 22, 35, 38 and 50 kg/ha.yr.

Alteration in soil macro fauna due to changes in vegetation succession

Since nitrogen is scarce in undisturbed drift sands, addition of nitrogen to the system due to increased airborne deposition will affect the vegetation and subsequently the food web. Effects of surplus nitrogen on vegetation succession are not completely clear yet. Although pioneer habitats seem to stabilise earlier because of increased algal growth (Pluis 1988) and a faster succession of vegetation and development of soil is suggested (Bakker *et al.* 2003), there seemed to be no difference between the speed with which open drift sands close by vegetation succession between areas with high (50 kg/ha.yr) and relatively low nitrogen deposition (22 kg/ha/yr) (Nijssen *et al.* 2010). However, succession speed was most probably already increasing in all examined areas, since critical levels of N-deposition for drift sands are far lower than 22 kg/ha.yr, as for calcium poor coastal grasslands (Remke 2009). Nitrogen deposition levels of 30 kg/ha.yr and more facilitate the invasive moss *Campylopus introflexus*, which completely replaces haircap-moss *Polytrichum piliferum* as well as lichen rich grasslands. These changes in vegetation succession alters soil macro fauna, as is shown in figure 14.5. At sites lowest in N-deposition (22 kg/ha/yr), the abundance of soil macro fauna is highest in lichen-rich grasslands. Density as well as feeding guild diversity decreases in lichen rich vegetation with higher N-deposition (35 kg/ha.yr), while this vegetation type is completely absent with high N-deposition (50 kg/ha.yr). The density of soil macro fauna is low in *Campylopus introflexus* with low N-deposition, when it only grows on decaying litter in forest clear-cuts. When N-deposition increases, densities of soil macrofauna also rise, with an alteration from moss-eating species (bryovores,
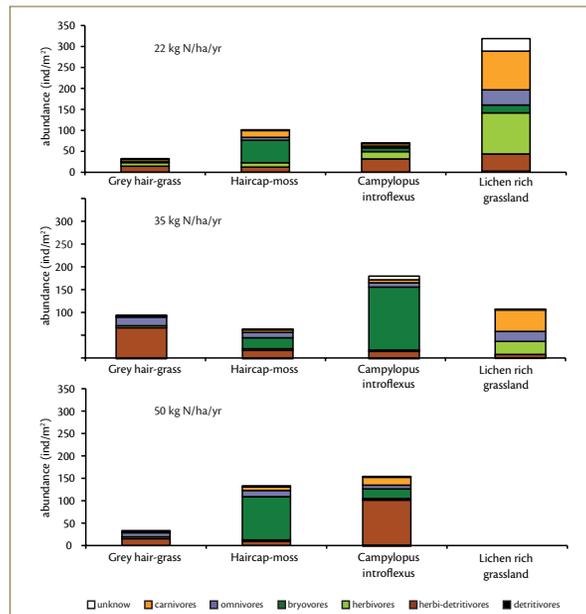

FIG. 14.5 Alteration of mean abundance (N=9 per treatment) of feeding guilds in soil macro fauna in a vegetation gradient within drift sands (after Nijssen *et al.* 2010). Note that lichen vegetation does not occur at N deposition of 50 kg/ha.yr.

mainly larvae from the snow scorpion-fly and Byrrhidae beetles) towards herbi-detritivores, mainly larvae of Tipulidae. Diversity of feeding guilds does not seem to change within vegetation of grey hair-grass and haircap-moss, but densities may increase with higher N-deposition.

Cumulative effects on the food web

As described above, fauna of drift-sand ecosystems are affected by high nitrogen deposition via several indirect ways. Besides altering vegetation composition and triggering changes in soil faunal communities within vegetation types, increased

nitrogen deposition has a negative effect on food quality of grey hair-grass, the main herbivore food source. Studies on the diet of northern wheatear show availability of soil fauna to be insufficient for raising offspring in drift sands, while it is sufficient in coastal dunes (Nijssen *et al.* 2010). Availability of prey species in the soil is high in early spring, but decreases quickly over the season. In the only vital inland remnant population (Aekingerzand, the Netherlands), adult wheatears depend mainly on caterpillars and grasshoppers for rearing their young. However, this population is situated in a part of the Netherlands with the lowest N-deposition (22 kg/ha/yr), while all populations in areas with high N-deposition are extinct or dramatically declining. As shown before, high N-deposition can result in high mortality (because of a more humid or less warm microclimate) and low body weight of invertebrates (due to low food quality of host plants), which means that alternative prey abundance and biomass is less available for insectivorous birds. These cumulative effects on food supplies might very well be the main reason for decline of the northern wheatear and extinction of the tawny pipit in the Netherlands. This would also support the findings of Bijlsma (1992), who noticed that decreasing population size of tawny pipits was correlated with a strong increase in territory size, possibly caused by low densities of suitable prey (see also Van Turnhout 2004).

Summarizing in relation to drift-sand management

Inland drift-sand landscapes are comparatively poor in biodiversity, but the occurring animal species are very characteristic for that biotope. Up to 4.4% of 3700 animal species, whose distribution in the Netherlands was analyzed, are significantly associated with drift sands; many of these species are rare and assigned to Red Lists in several NW-European countries. Tree grayling, and Eurasian wryneck are nowadays strictly associated with drift sands in the Netherlands and several other species hardly occur in any other habitat, such as the tawny earwig, ladybird spider *Eresus sandaliatus* and her parasite the wasp-spider *Eofeorola rhombica*. Coastal dunes also hold populations of the northern wheatear (photo 14.5), though inland populations are only found in drift-sand areas. Two other species strongly associated with the drift-sand landscape, the tawny pipit and great grey shrike, recently went extinct in the Netherlands, though there are still small populations in (former) military training areas in Germany (photo 14.1). Summarizing, drift sands play a significant role in the maintenance of faunal diversity in North-western Europe.

The association of characteristic drift-sand species has become stronger in the past decades. This is found both in the analysis of standardized distribution data based on square kilometers, as well as in the analysis of more precise descriptions of the biotope of species presently seen as typical for inland drift sands, like the tawny pipit, great grey shrike and tree grayling, All of these species occurred in earlier days

in various dry open landscapes in the Netherlands, such as dry heathlands, extensive dry arable land and river dunes. All vanished in these biotopes and are presently restricted to drift sands. Drift sands thus function as a refuge, which makes conservation and restoration even more important, though it might well be that this habitat is in fact suboptimal for some of these species. Restoration of degenerated sandy biotopes outside drift sands will, in that case, be necessary for durable conservation of the populations.

An important threat to drift-sand fauna has been the decrease of open drift-sand area, and subsequent fragmentation of drift-sand sites, in the last century. Threats to drift-sand fauna in remnant areas all have in common that they mitigate the extreme conditions of the original ecosystem, involving aeolian activity and extreme microclimate as well as low food supplies.

Mitigating factors include (former) stabilisation and forestation of drift sands, and increased airborne nitrogen deposition. It should be realized that most characteristic

Photo 14.5 **Northern wheatear (*Oenanthe oenanthe*) used to be a common breeding bird in many dry open habitat in the Netherlands. Nowadays inland populations are almost strictly bound to drift-sand areas (photo Harvey van Diek).**

animal species of drift sands are survivors, not competitors. Due to many physical, physiological and behavioural adaptations, these species have been able to develop life-history tactics with which they withstand the effects of drought, extreme temperatures, unpredictable movement of sand and a limited amount of food. When these conditions are mitigated, the advantages for characteristic species disappear and more competitive animal species as well as infectious fungi and bacteria increase. It is hypothesized in this chapter that a major threat to species originating from eastern 'steppe' landscapes is increased mortality (mainly in winter) due to a more humid microclimate, while lowering of the total temperature sum by encroachment of trees or dense grasses, and the formation of organic soil layers will be the biggest threat for species of southern 'Mediterranean' origin. It is obvious that global climate changes will also affect population dynamics of drift-sand species, however prognoses on the species level are most uncertain. One of the most surprising new insights is the decrease in food quality of grey hair-grass due to high nitrogen deposition. The mechanisms behind these effects and solutions to this problem are yet to be illuminated, though burial by sand due to aeolian dynamics can force the grasses to grow, thereby increasing food quality again.

Strategies for restoration and management of drift-sand landscapes are discussed in chapter 19. Here, some complementary advices can be given for restoration and conservation of drift-sand faunal communities. As shown in this chapter (and in chapter 9 for soil fauna), characteristic animal species are not proportional nor randomly distributed within the drift-sand landscape. Depending on their specific set of traits, forming a life history-strategy, species make use of a restricted part of the drift-sand landscape, or in some cases depend on several biotopes – for instance breeding and foraging area – between which they migrate. This implies that, to conserve or restore a complete drift-sand faunal community, managers should focus on the whole gradient of dynamic bare sand to lichen-rich stable biotopes. Another important remark is that remnant populations of characteristic species can disappear due to large scale management. Since many species, especially those which are typical for stable biotopes within drift sands, have lost their ability of flight, recolonization after management is most uncertain. Therefore, it is very important to make an initial research or proper inventory before restoration plans are made, l*et al*one measures are excecuted. This research will also help to make a proper diagnosis of specific problems within the area and may act as a start of monitoring the effects of these measures.