The relative importance and biological significance of non-stop and intermittent flight strategies in bird migrants crossing the Sahara

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I

I GENERAL INTRODUCTION

1. Background

Migration is a widespread survival strategy to exploit regularly changing occurrence of high food levels in certain areas (Terrill 1990). It occurs in many different taxa. In birds, it is generally defined as the seasonal movement from breeding to non-breeding grounds (Schüz 1971). Birds exploit temporarily nearly all different geographical areas even those offering only short times of favourable conditions (Berthold 2001). Many birds carry out long distance migration and cross ecological barriers, such as mountains, oceans, and deserts (Snow 1953; Moreau 1961; Haas & Beck 1979; Bairlein *et al.* 1983; Bairlein 1985b; Bairlein 1988b; Biebach 1990; Bruderer & Jenni 1990; Johnson & Herter 1990; Williams & Williams 1990; Biebach *et al.* 1991; Biebach 1992; Spina *et al.* 1993; Spina *et al.* 1994; Spina & Pilastro 1999). Birds of the Palaearctic-African migration system must deal with these three different types of obstacles in succession (the Alps, the Mediterranean Sea, and the Sahara) (Moreau 1972). Crossing of ecological barriers is mainly influenced by environmental factors, such as topography (Alerstam 1976; Bruderer & Jenni 1990; Bruderer 1996a; Bruderer 1997a; Zehnder *et al.* 2001), wind conditions (Alerstam 1976; Bruderer & Jenni 1990; Bruderer *et al.* 1995b; Liechti & Bruderer 1998; Liechti *et al.* 2000; Liechti 2006), and water stress (Carmi *et al.* 1992; Carmi & Pinshow 1995; Klaassen 1995; Klaassen 1996; Klaassen *et al.* 1999; Klaassen & Biebach 2000; Liechti *et al.* 2000; Klaassen 2004).

Migration systems being shaped by natural selection will be influenced by the change of environmental parameters (Berthold *et al.* 1992). An important topic is, how evolution has favoured certain behavioural patterns and to what extent such behaviour is genetically determined (Salewski & Bruderer in press). One interesting complex of questions deals with the behaviour of birds when they cross ecological barriers. Do they fly non-stop across such regions? Or do they fly a certain time, then land to rest in appropriate areas and start migration again after having recovered? Or do they make detours (Alerstam 2001)? Which factors govern the altitudinal distribution of migrants? Ecological barriers offer opportunities to examine such behavioural patterns. Within the Palaearctic-African migration system, migratory behaviour has been studied in the area of the Alps (Bruderer 1978; Bruderer & Jenni 1988; Bruderer & Jenni 1990; Liechti *et al.* 1995; Bruderer 1996a; Liechti *et al.* 1996; Zehnder *et al.* 2001) and around the Mediterranean Sea (Moreau 1961; Casement 1966; Biebach *et al.* 1991; Hilgerloh *et al.* 1992; Spina *et al.* 1993; Spina *et al.* 1994; Liechti *et al.* 1997; Pilastro *et al.* 1998; Bruderer & Liechti 1999; Spina & Pilastro 1999; Meyer *et al.* 2000; Rubolini *et al.* 2002). Deserts are supposed to be severe ecological obstacles due to extreme climatic conditions and only restricted occurrence of water, food and shade (Moreau 1961). Important studies on bird migration across the deserts of Israel have been presented by Bruderer (1994), Frumkin *et al.* 1995, Bruderer 1996b, Liechti & Bruderer 1995 and Bruderer *et al.* 2000). However, the Sahara is a far more extended and severe desert than the Negev and offers the opportunity to investigate how migrants cross such extreme barriers. Ground observations have already revealed some interesting behavioural adaptations of passerines, e.g. Bairlein *et al.* (1983), Bairlein (1985b), Biebach *et al.* (1986) and Bairlein (1988b).

2. State of art

According to Moreau (1961, 1972) the Sahara is such an inhospitable area that the few oases could not function as sufficient refuelling sites for all palaearctic migrants. Therefore, he assumed, that trans-Sahara migrants cross the desert in one large hop (lasting probably 40 to 60 hours). His suggestion gets support by the fact that intensive refuelling occurs in Northern Africa in autumn (Odum 1963; Bairlein 1988a; 1988b); this in turn confirms the notion that landbirds achieve a maximum departure fuel load when reaching the point to cross a barrier (Gifford & Odum 1965; Marsh 1983; Dierschke *et al.* 2005). Moreau's idea was later promoted by Lövei (1989) but without any new evidence. Calculations of Moreau (1972), Wood (1982), Biebach *et al.* (1986), Biebach (1990) and Rubolini *et al.* (2002) showed that crossing the Sahara might be possible with the available fuel loads. A moon-watching study at the northern edge of the eastern Sahara during autumn suggested that a certain proportion of migrants might cross the Sahara by a non-stop flight (Biebach *et al.* 1991). Later Biebach *et al.* (2000) estimated on the basis of a questionable radar study (see below), that about 20 % of all migrants show non-stop flights over the Sahara.

Most of the landed birds found in the Sahara during the day in autumn were in a good condition with high body mass and sufficient fuel loads; the proportion of lean and weak birds was rather low (Bairlein 1983; 1985b; 1988a; Biebach 1990; Bairlein 1992). Lean ones tend apparently to search for areas with vegetation where refuelling is possible, while fat birds were mostly found in shadowed places without feeding possibilities but with a reduced water loss during the day (Biebach et al. 1986; Bairlein 1988b). These fat birds seem to have sufficient fuel to migrate to the Sahel zone without refuelling (Biebach *et al.* 1986; Ash 1992; Biebach 1992). Therefore, the decision where to land seems to be strongly affected by the fuel stores of the birds. If most migrants followed the non-stop strategy, birds landing in the desert should be considered as exhausted "fallouts". However, the fact that most migrants were in rather good body conditions suggests the prevalence of an intermittent strategy (Biebach *et al.* 1986; Bairlein 1988b; Bairlein 1992). As birds making landfall in the Sahara during autumn migration belong to mainly two different types of body condition (lean or fat) and visit basically two different stopover sites (either rich feeding habitats or just shaded areas), it was assumed that the migratory strategy is modulated by the condition of the birds and is adjusted to environmental conditions (Gwinner *et al.* 1985; Biebach *et al.* 1986; Lavee & Safriel 1989). However, most passerines stopping-over at an oasis on the Sinai peninsula did not seem to adjust their stopover time in respect of body mass, i.e. energy reserves (Safriel & Lavee 1988).

Not only food, but also water is a rare resource in the desert and therefore, it was suggested, that migration should take place at night due to lower temperatures and less water consumption, whereas roosting in shaded areas during the day may be possible in spite of imminent dehydration due to extreme climatic conditions (heat and water deficiency) (Blem 1980; Austin & Miller 1982; Bairlein 1988b; Biebach 1990). Carmi *et al.* (1992), investigating the physiological limitations of flight duration of small passerines, claimed that the non-stop strategy is limited by water; birds are assumed to dehydrate, if they fly non-stop over the Sahara and therefore, non-stop crossing of the Sahara would be impossible for songbirds. This problem was mentioned earlier by Blem (1976), Biesel & Nachtigall (1987) and Biebach (1990); it was argued that a limitation of energy and water could be avoided by flying at higher altitudes, where air temperature decreases and water stress is lowered accordingly. However, Carmi *et al.* (1992) inferred that at high altitudes pulmonary ventilation has to be increased due to low oxygen pressure. Therefore, they pleaded for lowest flight altitudes to provide best conditions with respect to water balance. In contrast Liechti *et al.* (2000) showed, that adding water loss to models with tailwind as the only predictor of flight altitudes above the Negev does not increase the accuracy of the earlier predictions by Bruderer *et al.* (1995b). Wood (1989) pointed out that dehydration increases with time, implying that during a stopover without water intake, the water balance would deteriorate. He, therefore, favoured the non-stop strategy, because water needed during a stopover could be used more efficiently for flight.

Recent extensive wind tunnel experiments revealed that flying birds always experience a net water loss and that the exhaled air temperature has got a supreme effect on the respiratory water loss during flight. At least Rose coloured Starling (*Sturnus roseus*) cannot finish their 5000 km migratory flights without stopovers to refill water or particular behavioural adaptations to reduce water consumption (Engel 2005). This controversy on water balance of migrants crossing the Sahara suggests that other factors might also be important. Alternatively, flights may be restricted to night time due to diurnal air turbulence increasing the energetic costs of flying over deserts as well as in temperate areas (Kerlinger & Moore 1989).

Despite the controversy whether birds are able to fly for such long time, passerines were detected to climb up to 3000-6000 m to enter the trade wind zone south of Bermuda to cross more than 3000 km of ocean from northern America to the Caribbean and South America (Richardson 1976; Richardson 1980) and cross the Gulf of Mexico (Gauthreaux, Jr. 1971), reviewed by Williams & Williams (1990). Furthermore, Greenland Northern Wheatears (*Oenanthe oenanthe leucorhoa*) may perform extraordinary non-stop migratory flights between the breeding areas and south-western Europe (Ottosson *et al.* 1990; Dierschke *et al.* 2005; Thorup *et al.* 2006). These data indicate that songbirds are capable to cross such long distances non-stop at least under special wind conditions. Bruderer (1994), Bruderer & Liechti (1995) and Bruderer *et al.* (1995b) emphasised the importance of wind conditions for the energy balance and time consumption for migration. For the trade wind zone they consider the choice of altitude according to favourable winds to be the most important energy, time- and water saving flight tactic. According to them the intermittent strategy is maintained as long as favourable winds are available for flying and reasonable stopover sites (such as in semi-desert) for resting. They observed, however, non-stop flights of some wader-type birds above the Arava Valley (Israel) (Bruderer 1994); some of them making use of extremely strong winds, such as low jet-streams (Liechti & Schaller 1999).

Although songbirds seem capable to perform long flights, Bruderer (1994) and Bruderer & Liechti (1995) observed a distinct gap between nocturnal and diurnal migration in the Negev desert. Passage of migrants occurred nearly continuously throughout the night and ended at sunrise. Thus, in the Negev desert nearly all passerine migrants prefer an intermittent strategy (Bruderer 1994).

In spite of much research on bird migration across the Sahara, e.g. Kiepenheuer & Linsenmair (1965), Moreau (1967), Grimes (1973), Bairlein *et al.* (1983), Bairlein (1985a), Biebach *et al.* (1986), Bairlein (1988a), Biebach (1990), Biebach *et al.* (1991), Ash (1992), Bairlein (1992), Kjellén *et al.* (1997), Klaassen & Biebach (2000) and Biebach *et al.* (2000), there are more indications rather than real data about how birds cross this desert. Furthermore, the vast majority of work done in the desert concentrated on birds on the ground. These represent only an unknown fraction of the migration aloft. Bird passage has to be quantified up to the upper flight altitude of birds, otherwise the results are difficult to evaluate. Radar is a widely accepted tool to collect such data, but substantial attention must be paid to appropriate recording and cautious interpretation of radar data, e.g. Sutter (1957), Gehring (1963), Bruderer (1971), Bruderer et al. (1995a), reviews by Eastwood (1967) and Bruderer (1997b, 1997c).

Biebach *et al.* (2000) did some radar studies on passerine migration in the Egyptian Sahara; but there are methodological shortcomings that make at least parts of the results questionable. First, data were recorded differently at different sites. The detection probability of the radar for birds and insects had not been tested. A sensitivity time control (STC) to reduce clutter by small targets such as insects (Bruderer 1997b) was not described but probably present with an unknown effect. It was assumed that insect contamination had little effect on the results, but actual insect occurrence was never studied. The shape of the radar beam was not determined, and thus the surveyed volume, i.e. the volume scanned by the radar beam, remained unknown, so that no absolute numbers of migrants can be estimated. Even the relative comparisons they made were wrong, because they did not consider that the detection probability changes with distance and elevation. As no records of wing-beat pattern exist, it was impossible to distinguish between different bird guilds or even birds and insects. The operational range for small birds of 3 km was an estimate, small and large birds could not be distinguished since there was no distance dependent compensation of echo sizes (according to the r^4 law) (Bruderer et al. 1995a). Waterbirds and waders migrating non-stop over the area could have influenced the data, although the authors have neglected this, since “visual observation for many years at potential stopover sites, such as small lakes, produced only very small numbers” of these bird species. The quantitative estimate of migration densities in this radar study results in figures which are 10 – 20x and 20 – 40x higher than those of moonwatching observations by Biebach *et al.* (1991) at the same site and Kiepenheuer & Linsenmair (1965) at various sites in the eastern Sahara, respectively. Simply neglecting the different detection probabilities and not identifying the echoes at least at the insect/bird level will produce data, which is very difficult, if not impossible, to evaluate.
Thus, the controversies about the Sahara crossing remained unsolved:
(1) Do passerines cross the Sahara by an intermittent or non-stop flight?
(2) If the intermittent strategy is predominant, as in Europe, what is the biological meaning of restricting migratory flights to night-time?

3. Study

To answer these and other questions about Sahara crossing the Swiss Ornithological Institute carried out a bird migration study in Mauritania. Mauritania being surrounded by Senegal, Mali, West-Sahara and the Atlantic is characterised by a moisture gradient decreasing from the coast towards the eastern sand deserts. The south of Mauritania gets some precipitation through the influence of the Intertropical Convergence Zone in summer. Therefore, the Sahel savannah is greener in autumn compared to spring. In spring, migrants face desert conditions as soon as they leave the Senegal River valley, but profit from the vegetation-rich Mediterranean area.

An extensive radar and ground study was conducted during two spring seasons in 2003 and 2004 and during one autumn season in 2003 to investigate bird migration across the Sahara. A desert radar station, being run permanently at an inland oasis, as well as a mobile radar station moving from the coast as far east as possible were operated. The desert station was installed close to an oasis east of Ouadâne (20°56’ N; 11°35’ W), which lies isolated within the desert, in spring and autumn. It provided continuous data on the course of migration across this part of the Sahara. From the mobile station we analysed only data from the plain desert in the far east of Mauritania close to the border of Mali. The mobile radar stayed far north of Oualâta, at the southern edge of the extended deserts of El Djouf, at Mohammed Lemna (18°35’ N, 08°38’ W) in autumn 2003 for eleven days and near Bîr Amrâne (22°47’ N, 08°43’ W) in spring 2004 for about three weeks.

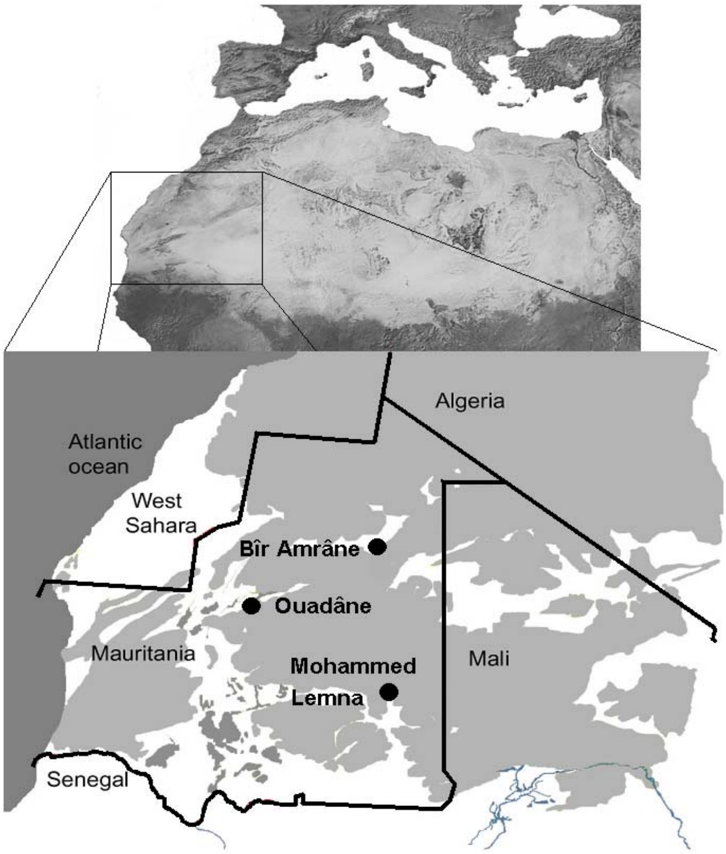

Figure 1. Location of the study sites in Mauritania. The upper map provides an overview of North-Africa. In the graph below Mauritania is enlarged and the three studies sites are indicated by black circles.

Ouadâne is surrounded by an ecological barrier, which extents 250 km south towards the Sahel savannah. The extreme sand desert sites of Bîr Amrâne in spring and Mohamed Lemna in autumn were prone to detect a high proportion of non-stop migration, if it occurred. Since there are no resting sites in the approach areas, these two sites are the places to prove, whether non-stop flights are a common feature and widely used migratory strategy to cross the Sahara. A comparison between the diurnal course of passerine passage at the fixed station in Ouadâne and the one collected by the mobile radar to the far east will indicate to what extent non-stop and intermittent migration vary along this west-east gradient.

Furthermore, intensive ornithological ground observations, including trapping and transect counts, were carried out in 2001, 2003 and 2004. As field observations in this region of Africa are largely lacking, the project contributed substantially to a better understanding of the avifauna in Mauritania (Salewski *et al.* 2003; Salewski 2004; Salewski & Martignoli 2005; Salewski *et al.* 2005; Schmaljohann & Salewski 2005; Schmaljohann & Thoma 2005; Salewski & Herremans 2006).

4. Outline of the thesis

To quantify bird migration properly, a sophisticated method is required. We used the well-developed radar system of the Swiss Ornithological Institute and improved the method for quantification. We applied a fixed beam measurement similar to the one already described by Bruderer (1971) (Fig. 2), which we improved in such a way that the echo signature of every echo was registered.

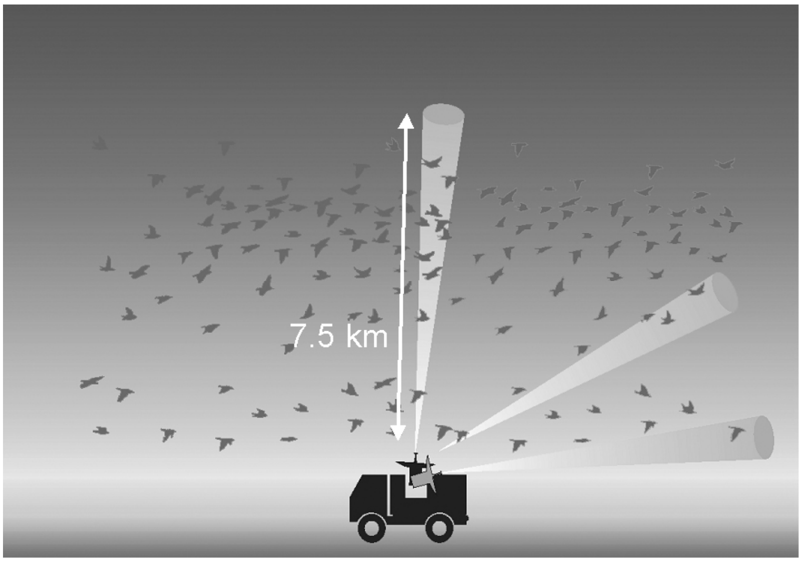

Figure 2. The fixed beam measurement. The beam of the radar was adjusted at different elevation angles to provide samples of birds in a half-shere around the radar. Maximum detection distance is set to 7.5 km.

The echo signature of birds corresponds largely to their wingbeat pattern (Bruderer 1997b), which differs from the one of insects by frequency, amplitude and overall pattern. Birds can be assigned to four major wingbeat classes: continuous flaps [“wader-type and waterfowl”], regular alternation of flaps and breaks as intermittent flight [passerine-type], intermittent with long, irregular breaks and flapping phases [“swifts”] and others [mainly soaring birds] (Bruderer *et al.* 1972; Bloch *et al.* 1981; Bruderer 1997b; Fig. 2). Furthermore, we had to define the surveyed volume depending on the actual echo sizes (which in turn depend on the distance and the elevation of the radar beam). We estimated for the first time different detection probabilities according to echo size and position of the bird within the radar beam. Our analyses show that neglecting the variations in detection probability may cause density estimations deviating up to 400 % from realistic values (**Chapter II**).

The vast majority of the trans-Sahara migration consists of songbirds (Moreau 1972), and therefore, we will mainly concentrated on this taxonomic group. Passerines can be divided into diurnal and nocturnal migrants. Nocturnal migrants outweigh diurnal migrants by far, constituting 85 to 90% of all passerine trans-Sahara migrants (Meinen 2004). To find out whether passerines migrate non-stop or intermittently across the Sahara, migration must be quantified over time of day, as stated above. Before any conclusions can be drawn from this temporal pattern, it must be investigated whether daytime passerine migration consists of diurnal migrants or of nocturnal migrants prolonging their flights into the day. A comparative analysis of radar data and intensive ground observations provided evidence that the observed daytime migration consisted to a very high degree of nocturnal passerine migrants (**Chapter III**).

Thus, we can apply the temporal pattern of passerine migration to answer the core question about the relative importance of non-stop and intermittent flight strategies. Most passerines cross the Sahara by nocturnal flights and diurnal rests; the intermittent migration is the predominated flight strategy! However, in nutrition terms they are exposed to similar conditions as in a long non-stop flight, because most of them rest in the bare sand desert and do not encounter food or water during their daytime stopovers (**Chapter IV**).

Meteorological conditions have a paramount effect on the migration behaviour, e.g. Carmi *et al.* (1992), Bruderer *et al.* (1995b), Liechti *et al.* (2000), Erni *et al.* (2005), Engel (2005) and Liechti (2006). However, the question whether a passerine chooses its flight altitude to minimize the energy or water consumption when crossing the Sahara, is not yet settled (Liechti *et al.* 2000; Klaassen & Biebach 2000). It was assumed, that energy and water demands would be opposite in spring due to favourable winds high up and moderate temperatures together with high oxygen pressure at low altitudes (Klaassen 1996). We, therefore, compared altitudinal distribution of passerines with model predictions considering energy as well as water/energy consumption (Pennycuick 1989; Carmi *et al.* 1992; Klaassen 1995; Klaassen *et al.* 1999). Nocturnal passerines seem to migrate mainly at altitudes, where they can minimize their energy expenditure, but the results remained unsatisfying, because predictions of the two models did not differ significantly (**Chapter V**).

Since most passerines migrate exclusively at night (Chapter V; see also Bruderer & Liechti (1995,1999) and Meinen (2004)), there must be factors acting upon migrants preventing them from daytime flights. If songbirds extend their migratory flights only under certain conditions into the day as in the Sahara (see Chapter IV), it might be possible to draw conclusions about the reasons why long-distance migrants among the songbirds do usually not migrate in daytime. Prolongation of nocturnal flights into the day was more often observed in spring than in autumn. In spring, birds profited from tailwinds (anti-trades) when flying high and additionally from low temperatures. In autumn, when they made use of the trade winds at low levels with temperatures above 30°C, migration was highly restricted to nighttimes. We analysed autumn and spring flight altitudes for night- and daytimes in respect of their energy and water consumption. During nights, the distribution of tailwinds explained best the passerines' altitudinal distribution, while assumed water stress had no influence on flight altitudes. Passerines prolonging their migration into the day selected higher altitudes for flying than at night, either due to water stress or to avoid strong air turbulences decreasing with altitude. Prolonged flights at low altitudes in autumn were probably more costly than diurnal flights in spring and were, therefore, a rare event (**Chapter VI**).

Anatidae and Charadriformes prefer special habitats for resting and refuelling, that are basically missing in the Sahara: wetlands! One might assume that these birds avoid crossing the central Sahara, but there are a some records right from the middle of the Sahara, e.g. Moreau (1967), Grimes (1973), Bairlein *et al.* (1984) and Salewski *et al.* (2005). Therefore, these wetland-dwelling birds do indeed cross the central desert, but it is still unknown to what proportion they fly directly across or along the coast. We observed waders passing solitarily the study site at night and in flocks during the day. However, quantification of diurnal wader migration remained a problem, because it is not trivial to calculate migration densities from radar data based on flocks. Due to the first and therefore, surprising observations of large Laridae flocks (Lesser Black-backed Gulls, *Larus fuscus*) crossing the Western Sahara, we described here these observations (**Chapter VII**). Due to their special flight performance (fast fliers), the deficiency of roosting sites within the Sahara, and their potential to use strong tailwinds, they can achieve very high migratory velocities (Liechti & Schaller 1999) enabling large Gulls to cross the Sahara non-stop. Anatidae and Charadriformes possessing similar flying power are suggested to use similar desert crossing strategies.

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II

Quantification of bird migration by radar – a detection probability problem

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Quantification of nocturnal bird movements has been an aim of radar ornithology since almost sixty years. Besides the scientific interest, there is an increasing need to quantify bird migration for the assessment of bird collision risk with man-made structures. To assess collision risk, radar is often chosen to provide the required data. While for many scientific investigations relative figures were sufficient, collision risk inquiries aim at absolute values. However, in many environmental impact studies, the radar method was used in an astonishingly careless manner. The processing of echoes consisted mostly of counting blips within defined screen fields, and the surveyed volume was often estimated without reference to the detection probabilities of different echo sizes. This article outlines for the first time a method how radar data can be analysed to achieve reliable estimates of true numbers of birds aloft. This mainly involves excluding insect echoes and estimating different detection probabilities according to echo size and position of the bird with respect to the radar beam (aspect). Our analyses show that neglecting the variations in detection probability may cause density estimation to be wrong by 400 %. We fear that quantification of migration and the predicted number of birds affected by collisions with man-made structures are in many cases based on unreliable figures.

Keywords: bird migration; radar; echo identification; detection probability; quantification

Introduction

Quantification of bird migration is an obvious aim of studies dealing with the temporal and spatial distribution of bird migration. Because birds migrate too high for visual observations and the majority of migrants flies at night (Bruderer & Liechti 1995, 1999), radar is a widely accepted tool to collect such data (Bruderer 1997a, 1997b). Scientific studies paid usually considerable attention to appropriate recording and cautious interpretation of radar data, e.g. Sutter (1957), Gehring (1963), Bruderer (1971), Buurma (1987, 1995), Bruderer *et al.* (1995) and reviews by Eastwood (1967) and Bruderer (1997a, 1997b). The need for quickly available results for environmental impact studies and the recent off-the-shelf availability of cheap ship radars led various groups to start radar studies without sufficient concern about the problems of such instruments. The highest demand for environmental impact studies is currently connected to off-shore wind farms (Harmata *et al.* 1999, Hüppop *et al.* 2004, Desholm & Kahlert 2005, Hüppop *et al.* 2006, Desholm *et al.* 2006). To assess the significance of potential bird collisions, bird movements have to be quantified. The principle of quantification seems simple: the number of birds within the radar beam provides the spatial and temporal distribution of birds. However, to achieve a reliable result, echoes must be identified as birds and the surveyed volume must be known, which makes the quantification of migrants a rather difficult task. The present paper aims to revive former working standards of radar ornithology, and to depict a new method for the quantification of bird migration.

Insects, bats and birds embody the most important biological radar targets. Insects can make up an overwhelming part of echoes depending on time, location and radar sensitivity (Riley & Reynolds 1979, 1983). While bats are only of minor quantitative importance in comparison to birds (Bruderer & Popa-Lisseanu 2005), insect echoes present the most significant interference with bird echoes. The identification at the bird-insect level is mainly based on echo signature, air speed and echo size (Gehring 1967, Bruderer 1969, Riley 1973, Larkin 1991) and was considered in some studies (Bruderer 1971, 1994, Komenda-Zehnder *et al.* 2002, Gauthreaux *et al.* 2003, Diehl *et al.* 2003). Due to differences in wingbeat pattern, birds could be divided into different bird classes (wader -, passerine - and swift - types) and assigned to different body sizes according to wingbeat frequencies (Bruderer *et al.* 1972; Bloch *et al.* 1981).

The size of the surveyed volume, i.e. the volume scanned by the radar beam, is probably the most critical factor for calculating real bird densities. As for all monitoring methods, the detection probability is essential. In radars it depends on the size of the echo produced by a target. The actual echo size is determined primarily by the distance to the radar and the size of the object, then by the aspect (the alignment of the body axis with respect to the radar beam: lateral, ventral, frontal or caudal view), and the position of the object in the radar beam (centre or margin) (Edwards & Houghton 1959, Eastwood 1967, Bruderer 1971, Bruderer *et al.* 1995, Buurma 1995). In contrast to optical devices (e.g. telescope) the radar beam width depends on the echo size. Therefore, specific detection ranges must be determined for different echo sizes, which complicates the calculation of the surveyed volume considerably. Although detection probabilities might be calculated theoretically (Riley 1979, Smith *et al.* 1993, Chapman *et al.* 2002), it is indispensable to reconsider this issue empirically. Liechti *et al.* (1995) showed, that the empirically determined radar beam width was two times larger than the suggested theoretical one.

Neither echo identification nor proper surveyed volume estimations were done in most radar studies, e.g. Cooper *et al.* (1991), Harmata *et al.* (1999), Biebach *et al.* (2000), Hüppop *et al.* (2006). Considering the demand for fast and cheap, but nevertheless reliable environmental impact studies, the importance of proper quantitative analysis cannot be overestimated. As these figures are the basis for nature conservation decisions the shortcomings of already published analyses are worrying. In this paper we present a general procedure how to estimate absolute bird densities based on radar data (Fig. 1). We stress the importance of proper echo identification and how echo size can be considered to estimate detection probability and to calculate bird quantities. Furthermore, we give an example of how this procedure can be applied to a specific radar system, discuss major and minor shortcomings and its application to other radar systems (Table 1).

The theory

Echo detection

Objects within a radar beam reflect some of the pulse energy back to the radar antenna. This received power at the antenna (without considering echo-processing within the radar) P_r is determined by the radar equation:

$$P_r = \frac{P_t \cdot G \cdot \sigma \cdot A}{(4\pi R^2)^2},$$

with P_t = transmitted power, G = antenna gain, σ = radar cross-section, A = surface of antenna and R = distance between antenna and echo, for further information see Eastwood (1967). Consequently, the echo sizes increase dramatically with decreasing distance (roughly by R^4). To avoid the detection of numerous small targets at close range (insect, sea waves or other ground clutter) most radar systems reduce the sensitivity of the receiver with decreasing distance. This device is called sensitivity time control (STC), which simply applies a distance dependent detection threshold. As the manufacturer rarely defines this built-in function properly, the reduced sensitivity of the system must be determined by calibration. By calibrating the system, echoes can be assigned to a certain echo size and, considering the distance to the radar, this allows to determine a standardized echo size, which is then independent of distance. Thus, the calibration provides the distance dependent detection range of given echo sizes (s. below).

This is essential, as the working range of most STC filters is within the range where generally most birds are counted. We will use the term “echo size” as a synonym for standardized echo sizes for the remaining text. Finally, an object detected by radar can be depicted by the following parameters: echo size and its variation in time (echo signature), position in space and its temporal variation (speed and direction).

Echo identification

Bird and insect echoes can be distinguished by differences in their echo signatures. For bird echoes it is assumed that the water in the birds’ body causes the main part of reflectivity. The rhythmic dilatation and contraction of the bird’s body causing variation in the radar cross-section and thus the typical echo signature of birds, which mirrors the wingbeat pattern (Bruderer 1969, 1997a). For insects, own (unpublished) experiments suggest that it is the chitinous coat, which reflects the radar waves, because dry individuals provided as good radar targets as living insects. This may be one reason for the complicated structure of insect echo signatures, which may consist of a mixture of wing movements with various other body movements. In general, the amplitude as well as its variation are much smaller in insect than in bird echoes (Gehring 1967, Bruderer 1969, Riley 1973). This is combined with relatively low air speeds of most insects (Larkin 1991), and the generally small echo size.

Quantification

The surveyed volume is a function of the distance dependent detection probability of different targets. While the beam shape is geometrically similar for all echo sizes, its absolute size varies with the echo size. Based on the maximum detection range for a given echo size, the absolute size of the surveyed volume can be calculated from the theoretical antenna diagram (specifications given by the manufacturer). To estimate the surveyed volume for a certain sample of different echo sizes, the surveyed volume for each echo size-class has to be determined and the frequency distribution of these echo sizes has to be identified (s. above for the need of calibration). Based on this frequency distribution of the echo sizes, a weighted mean surveyed volume can be calculated.

As the echo size depends on the radar cross-section (σ), the aspect at which a bird/target is seen by the radar has a strong influence on the echo size (Houghton

1969, Bruderer & Joss 1969). Therefore, we have to be aware that echo size distribution, and thus the surveyed volume, varies with the aspect.
Migration traffic rate (MTR) is an established measure of migratory intensity. It can be calculated either by counting birds within a known surveyed volume over a given time period, or by measuring actual echo distribution within a given volume multiplied by ground speed. The MTR is defined as the number of birds crossing a virtual line of one km perpendicular to the flight direction within 1 h, adapted to metric-system from Lowery (1951) by Bruderer (1971).

Radar measurements

An echo detected by radar can be characterized either by its echo size, echo signature, air speed, flight direction and/or distance to the radar. Up to now, no radar system has provided all these theoretically available parameters with just one single measurement method (Table 2). In the frequently used *horizontal surveillance mode* targets are usually hit several times by the rotating beam and thus, can provide information on echo size, distance, flight direction and ground speed. The accuracy of flight altitude depends on the beam width in the vertical plane and is generally very poor (except for the large and very expensive stacked-beam surveillance radars). To achieve altitudinal distributions small ship surveillance radars were used in a *vertical scanning mode*, e.g. Harmata *et al.* (1999), which can provide echo size, distance and height. *Conical scanning* with a pencil beam at different elevation angles, as used by Bruderer *et al.* (1995), can also provide echo size, distance and height. In *fixed beam measurements* echoes are counted over a given time period, without moving the radar beam. This can provide the echo size and its variation in time (echo signature), the distance and height. With all these methods a representative sample of echoes in space and time can be collected. However, for all these echo size estimates we must consider that targets were also detected at the edge of the beam and thus do not represent real target size. In the *tracking mode* a single target is kept within the centre of the beam for a given time, thus all the possible parameters mentioned above can be determined. However, a proper quantification is not feasible as the number of possible recordings is restricted by the tracking time, and the searching time per height interval is defined by the operator.

The application

The data

The data we present here was collected at the oasis Ouadâne in Mauritania, located 426 m above sea level (20°56’ N, 11°35’ W). The radar was operated from 06 March to 15 May 2003, 11 August to 25 October 2003 and 15 March to 10 May 2004 with a daily break of 2 h alternating daily from 12:00 to 14:00, 14:00 to 16:00 and 16:00 to 18:00 h, respectively.

To gain samples satisfying the major aspects mentioned above and to estimate absolute migratory intensities, we used a “Superfledermaus” X-band radar (peak pulse power of 150 kW) in a fixed beam and tracking mode (compare Table 2). The fixed beam measurements were carried out by sampling objects flying through the beam during 4 min (246 s) at a high (78.75°) and low (11.25°) elevation angle to cover a relative large surveyed volume at the different altitudes. The beam was directed towards west (270°), perpendicular to the main flight direction of the migratory birds. Echo signal strength of all targets crossing the beam within a distance of 200 to 7 500 m was recorded with a sampling rate of 130 Hz providing sufficient resolution to recognise wingbeat pattern of birds. The resolution in distance was 30 m.

In the tracking mode we aimed at recording a representative sample of flight directions, velocities and echo signature of individual targets (about 70 000 tracks). During daytime targets were visually identified using a 12.4x telescope mounted parallel to the antenna (n = 5 226). Based on wind profiles measured every 6 hours, air speed and heading were calculated for each track (Bruderer *et al.* 1995). Statistics were calculated using the statistical software package R.

Echo detection and standardization of echoes

The receiving system of the radar was calibrated at the beginning of each observation period with a signal generator (Radar Test Set 75, Gigaset) to convert the relative values produced by the raw video signal into dB-values. All echo sizes were standardized to a distance of 3 km, as follows:

$$\text{echo size} = \text{dB}_i + \log_{10}(R_i^4 / 3000^4) / \log_{10}(10) \times 10$$

with dB_i = received power from echo_i and R_i = distance in m. Based on these echo sizes corrected for distance, we applied a distant dependent threshold (STC), excluding all targets which would not be detectable at least up to 3 km (above the noise level threshold of –90 dB). The working range of the STC was defined empirically, with the aim to exclude the highest possible proportion of small echoes like insects, but the least possible proportion of small birds. As small birds like Goldcrests *Regulus regulus* can be tracked with our radar slightly beyond 3 km in tail-on view (own unpubl. data), we assumed that mainly clutter and insects and not birds are excluded. After applying the 3 km STC, echoes were recognized automatically by a tailor-made software (developed by EB). Echo signature, distance from the radar, time in the beam (echo length) and standardized echo size characterize each echo (s. below). Fig. 2 shows the difference between the raw radar picture and the same picture after applying a calibrated STC affecting echoes up to 3 km.

Echo identification

In a first step, visually identified echoes tracked during daytime were analysed. Based on these results we classified in a second step the rest of the individual tracks (mainly nocturnal ones) and all echoes recorded with the fixed beam measurements.

Bird-insect identification

Visually identified tracks of birds and insects differed clearly in the echo signature and main frequency of the signature. The birds had a main frequency of 8.8 Hz (sd = ± 3.8, *n* = 1 252) and insects of 17.1 Hz (sd = ± 24, *n* = 70), respectively (Mann-Whitney U-test: W = 5091.5, p-value < 0.0001). Furthermore, visually identified insects were characterized by their low air speed, relatively small echo size and low variation in echo signature (Fig. 3). However, based on the limited parameters available from fixed beam measurements (distance and echo signature), we were not able to define a satisfying mathematical algorithm to distinguish between birds and insects, and additionally, between different type of birds (see below). Therefore, all echoes, from tracks and fixed beam measurements were classified based on the echo signature by a skilled expert (HS), who got experience during 7 months of fieldwork, where he could train echo signature identification of diurnal tracks with parallel visual observations. Targets that could not be allocated to birds or insects were classified as unidentified flying objects.

Bird class identification

Among the birds, echo size varies considerably. By using the wingbeat pattern, bird echoes could be assigned to different bird classes: a) continuously flapping birds such as waders, waterbirds, small herons, rails, etc. (wader type) are detected over relatively large distances due to their relative stable average signal strength, b) intermittently flapping birds, mainly passerines without swallows and corvids (passerine type); over the Sahara these are mostly small birds, their detection probability being additionally reduced by the intermittent flapping mode, c) intermittently flapping birds with long and irregular flapping and pausing phase, such as swifts and bee-eaters (swift type); detection probability similar to waders, d) raptors, storks, large gulls and herons, etc. (large single birds); with very strong echoes, e) flocks of birds (only visually determined) and f) unidentified birds characterized by a strong echo intensity but no clear wingbeat pattern (unidentified birds), for further details about echo signature see Bruderer *et al.* (1972) and Bruderer (1997a). For the current analyses we considered only wader -, passerine -, and swift types.

Quantification

Detection range per echo size

As our echo sizes were based on calibrated dB-values, we only had to establish empirically the maximum detection for a single echo size-class. We chose the echo size-class with the highest number of echoes as the reference class, because the chance to record an echo at its maximum detection range increases with sample size (-78 dB → 5 970 m, Fig. 4). Based on this range the maximum detection range for the other echo size-classes could then be calculated as follows:

$$\text{maximum detection range}_{\text{echo size}_i} = \frac{\sqrt[4]{10^{\frac{\text{echo size}_i}{10}}}}{\sqrt[4]{10^{\frac{\text{echo size}_{-78\,\text{dB}}}{10}}}} \times \text{maximum detection range}_{\text{echo size}_{-78\,\text{dB}}} .$$

Frequency distribution of echo sizes

In the fixed beam measurement, birds fly across the radar beam at any (unknown) distance from the beam centre. Large targets grazing only the edge of the radar beam might produce lower echo signal strength than small targets crossing the centre. To achieve an echo size distribution representing the real size distribution of the targets, we had to find a way to select only those birds flying close to the centre of the beam. This was achieved as follows: (1) Echoes were only considered flying perpendicular to the radar beam (= no variation in distance), because mainly at low beam elevations the flight path length within the beam increases in birds flying at acute-angles to the beam. (2) Based on the tracking data, mean flight speed per night and 1000 m height intervals were calculated. (3) To estimate the distance a bird had covered in the fixed radar beam (its echo length), the mean flight speed per night and altitude was multiplied with the time the echo was recorded in the beam. (4) For each distance interval of 250 m we divided the assumed beam width of 3° into sectors of 1°. Additional sectors of 1° were added beyond the assumed 3° beam. Then the frequency distribution of the echo lengths based on these sectors was computed. (5) Finally, we chose from each 250 m distance interval the sector with the highest numbers of echoes as the one where most birds were flying across the centre of the radar beam. This procedure was chosen because the probability to cover a distinct distance across the radar beam, i.e. how far it is from the centre, follows the cosine function. E.g. the probability to cover a distance of less than 50% of the beam width corresponds to 1 – cos (30°) = 0.13. Dividing the beam width into thirds, provided expected probabilities of 0.06 for birds crossing less than one third, 0.20 for crossing between one to two thirds, and 0.74 for more than two thirds. Therefore, the beam width step with the highest frequency per 250 m distance interval comprised the birds flying close to the centre of the radar beam. Summarizing these beam width steps up to 3 km provided the distribution of the echo sizes. Only echoes within the working range of the STC (< 3 km) were considered, because within this range detection probability is constant for all targets.

Bird class variation and aspect

To account for major differences in echo sizes we considered three different bird classes (s. above). Furthermore, as the echo size varies also due to the aspect, we calculated separate echo size distributions for high elevation measurements (ventral view) and low elevation measurements (mainly lateral view). Thus, the bird sample was divided into six different subsamples (two elevations, each with three bird classes). A separate frequency distribution of echo sizes was calculated for each subsample. Within the same bird class the frequency distribution was significantly different between high and low elevations (Fig. 5).

Mean detection range

Based on the echo size distribution of the six subsamples weighed mean surveyed volumes were computed. The resulting volumes differed distinctly between the subsamples (Fig. 6). Surveyed volume of wader, passerine and swift types was 3.7x, 1.9x and 3.9x larger in high than in low elevation measurements, respectively (Table 3 and Fig. 6). The largest difference occurred between the surveyed volume for swift types in high elevation and passerine types in low elevation measurements (4.7x). For further calculations of migratory traffic rates, the beam width with respect to distance, resulting from the mean surveyed volume (Fig. 6), was approximated for each subsample by two mathematical equations; a linear regression up to 3 km distance and a polynomial of the 4th degree beyond 3 km.

Migration traffic rate

To estimate MTR at different height intervals, we have to take into account the surveyed volume per height interval (e.g. 50m). This area was approximated by multiplying the length of the radar beam by the mean beam width within a given height interval (Fig. 7). At low elevations the surveyed areas overlap notably with adjacent height intervals. This was ignored, because the position of each echo within the radar beam is only given by the distance. To calculate MTR the number of birds within each height interval was multiplied with the ratio between the surveyed area and the reference area of 1 km times the height interval (50 m). The surveyed area is only representative for birds flying perpendicular to the radar beam. To account for flight direction, we calculated mean flight direction per night and 1 000m height interval from the tracking data and corrected the surveyed area by the cosine of the average angle of incident with respect to the direction of the radar beam. Thus, MTR is based on the number of the birds crossing the beam, divided by the cosine-corrected surveyed area and the recording time. Bird density per km^3 can be obtained by dividing the MTR by the flight speed.

Discussion

Echo detection

A target will be detected by any radar system, if the reflected energy is above a certain threshold. Most commercial radar systems apply a sensitivity time control (STC) to mitigate the dramatic increase in signal strength with decreasing distance of the target. Unfortunately, the function of this device is almost never properly stated, neither calibrated and thus, the effect of the STC remains unknown. In addition, it is common practice in the field to reduce actual clutter (e.g. waves) by manipulating the STC to a degree where "birds could still be detected" (Cooper *et al.* 1991). This is not suitable as such a reduction always implies a decrease in the surveyed volume. E.g. reducing the sensitivity in our radar system by increasing the STC from 3 up to 4 km would reduce the surveyed volume by about 50%. Consequently, any change of the sensitivity within an observation period must be kept constant (Hüppop *et al.* 2004), otherwise even relative comparisons between single days or nights are dubious. This may be less critical in the vertical scanning measurements, because the beam width is of minor importance. Nevertheless, as the function of the STC is undefined and not necessarily linear, it is unknown whether the detection probability remains constant for all targets over distance. Obviously, a varying detection probability for different target sizes over distances will provide unreliable results.

Echo identification

Echo identification at least on the level of birds and insects is indispensable. Without an identification of the radar echoes, the validity of the results remains weak. Entomological radar studies have been carried out for a long time (Glover *et al.* 1966, Riley 1975) and radar as a tool for studying insect migration is widely accepted (Smith *et al.* 1993, Chapman *et al.* 2003). Unfortunately, insect presence was often just ignored in bird radar studies, even when using X-band radars, which are highly sensitive to insects, e.g. Harmata *et al.* (1999), Biebach *et al.* (2000) & Hüppop *et al.* (2006). Biebach *et al.* (2000) studying bird migration with an uncalibrated X-band radar in the Egyptian desert, estimated migration traffic rates which were almost two orders of magnitude higher than those obtained by Biebach *et al.* (1991) with moonwatching in the same area. Within our data from the desert, insect proportion varied from 16% to 75% between two seasons. Butterflies, dragonflies and moths are well known to migrate in large numbers between the North of Europe and tropical Africa (Johnson 1969). Although we can assume a decrease in the numbers of large aerial insects from south to north (at least within Europe) we must be aware of radar-detected swarms of mosquitoes even near the pack ice in the arctic up to heights of 800 m above ground level (Gudmundsson *et al.* 2002). Therefore, we have strong reservations that insects can be neglected in any study area without specifically checking the facts.

Bird-insect identification

The most reliable parameters for the bird-insect identification are echo signature and main frequency in the signature, because they are independent of wind speed and aspect and can be applied to the identification of tracked targets and fixed beam echoes in the very same way, see e.g. Glover *et al.* (1966), Bruderer (1969) and Riley (1973). To attain an identifiable echo signature, the recording time plays an important role. Theoretically, the recordings of one second or even a fraction of it are sufficient to detect single wingbeats. At least in our radar the variation in echo signature due to other factors than the wingbeat movement would rarely allow a reliable identification of such short echoes. We therefore accepted only echoes with a minimum recording time of 2 seconds.

Air speed seems to be a good parameter for the insect bird discrimination as well, since many insects do not possess an air speed higher than 5 m s^{-1} (Larkin 1991) and most birds not below 10 m s^{-1} (Bruderer & Boldt 2001), respectively. However, there are two problems: (1) Some insects, especially large moths and locusts, which are highly migratory, can achieve high air speeds of up to 9 (Waloff 1972) or even 11 m s^{-1} (migratory locusts; own unpubl. data), while some birds fly with air speeds clearly below 10 m s^{-1}, e.g. Goldcrest (Stark 1996). (2) The precision of air speed calculated from ground speed and the wind vector depends on the accuracy of these recordings. To avoid notable deviations in the estimation of air speeds, the wind measurements should be as close as possible to the recording of the targets. Our results show that even with quite precise data some, however few, overlap between air speed of insects and birds still exists (Fig. 8). Using mean wind conditions at specific pressure levels can be used only as a very rough estimate, resulting in very inaccurate approximations of potential insect contamination within a sample. To select for conditions with generally low winds based on ground level measurements (Williams *et al.* 2001) and then take ground speed as an estimate for air speed is unsuitable, as e.g. in our data low wind speed at ground (< 3 m s^{-1}) occurred during 60% of the days, while at the birds main flight level it was only 10% (and directions often opposite).

Identification of bird classes

Due to their wingbeat pattern birds can be assigned to different bird classes (Bruderer *et al.* 1972), but only when being detected solitarily (Bruderer 1971). Echo signatures of flocks are a mixture of various echo fluctuations and do not provide wingbeat patterns. While identification on the passerine type level is straightforward, differentiation of wader and swift types is dependent on the duration of recording (short tracks of swifts in flapping flight may be taken as waders). In our opinion identification at the species level is possible only for some special cases, e.g. Common Swift *Apus apus* in northern Europe (Bruderer & Weitnauer 1972). Nevertheless, there were attempts to identify tracks on marine surveillance radars to species groups by means of echo signature and ground speed (Harmata *et al.* 1999, Desholm & Kahlert 2005). Unfortunately, no detailed information about the actual discrimination parameters were given. Therefore it remains obscure, how echo signatures from flocks, hardly providing wingbeat patterns, and ground speed, highly dependent on wind conditions, can be used to discriminate between species.

Manual echo identification, as in our case, has the drawback that it is very time consuming, to a certain extent subjective, and expert knowledge is rare and costly. However, we hope that by making use of the ongoing developments in signal processing, we should be capable to build up a reliable algorithm for an automatic echo identification in future.

Quantification

Apart from the distinction between birds and insects, the definition of the surveyed volume is the most critical factor for quantifying bird migration. The composition of echo sizes has a distinct influence on the surveyed volume and thus, the estimated migratory intensities. To account for this, the radar and its operational beam width must be calibrated to compensate for the different detection probabilities (Bruderer *et al.* 1995). Calibration can be performed either by feeding a defined amount of energy

directly into the radar system (signal generator), or by measuring defined echoes at various distances in the field.
We estimated for the first time the surveyed volume based on the distribution of the echo sizes. The detection range varies largely between bird echoes (Fig. 6), and is highly influenced by the bird's aspect (in our data lateral and ventral, Table 3). Ignoring these differences and applying a surveyed space derived from lateral detection to high elevation measurements, would lead to an overestimation of bird densities in the vertical looking beam by 200 to 400 % (!). Differentiating between different type of birds (passerine, wader, swifts) provides not only more accurate migration intensities, but also allows to investigate differences in the temporal and spatial pattern of these groups. While few studies used a radar beam width based on empirical results (Liechti *et al.* 1995), most radar studies just applied the beam width given by the manufacturer, without any knowledge about the range and the form of the STC-function. In such cases even relative comparisons are dubious, because the increase in the surveyed volume with distance is underestimated at close range and overestimated at long range (Fig. 6). Therefore, for any fixed beam or conical scanning (incl. horizontal scanning) method it is indispensable that the surveyed volume is estimated accordingly.

An alternative approach was propagated by Harmata *et al.* (1999) and Hüppop *et al.* (2004) for vertical scanning ship radars, where the targets are detected when flying across the vertically rotating beam. In this case the radar beam width can be neglected, if the time of recording and the rotational speed guarantees that all targets are hit at least once close to the centre of the beam. To account for the decreasing detection probability with distance they calculated correction factors based on the distance sampling method (Buckland *et al.* 2004). For this calibration only birds within a single height interval (100 to 200m) were selected, assuming that the horizontal distribution of migratory intensity is homogenous. Applying these correction factors to all elevation angles of vertical scanning measurements is leading to two problems. (1) The increase in the detection probability from lateral to ventral aspect was ignored (Tab. 4 and Fig. 6) resulting in an overestimation of the densities at high elevations. (2) There are clues that large waterbirds tend to fly lower over sea than small songbirds (Klaassen 1996; Pennycuick *et al.* 1999). Thus, the correction factors are biased towards large birds, resulting in an underestimation of the number of small birds flying high. Moreover, this is a violation of the distance sampling method as the detection probability should vary only with distance and not between individuals. Although this seems to be the most advanced method used with ship radars, even relative comparisons between different altitudes within the same time period have to be treated with caution.

We do not enter to the theoretical approaches for data analysis used by Drake (1981) and Smith *et al.* (1993), respectively, because some assumptions in their methods violated the actual conditions: e.g. they can only be applied to vertical beam measurements, echo size was not considered, in spite of extreme size-dependent variation in echo size for objects smaller than the wave length (Eastwood 1967). In spite of these problems, the method of Smith *et al.* (1993) was later applied in entomological studies (Chapman *et al.* 2002, Chapman *et al.* 2003).

Flight direction

For any kind of density measurements flight directions have an important impact on quantifications. In conical (and horizontal) scanning, detection probability varies strongly with the scanning angle due to the changing aspect of the migrants. Mostly, migration is concentrated along a specific flight direction, hence the number of detected echoes on the radar screen is largest along the axis perpendicular to the main flight direction; echo sizes produced from lateral view are larger than from frontal or caudal (Bruderer & Joss 1969, Bruderer *et al.* 1995). In fixed beam and vertical scanning measurements, the influence of the aspect and thus flight direction is similar to conical scanning. Additionally, the surveyed area must be calculated with respect to the flight direction. Positioning the fixed beam (or the plane of the vertical scanning) at the right angle to the main flight direction provides the maximum surveyed area, e.g. at zero angle the surveyed area is minimal and at 30° it will be halve. Flight directions can be obtained from target tracking or with a horizontal scanning method. Horizontally scanning is restricted to low altitudes; extrapolation to higher altitudes is inappropriate, because different migrants might prefer different altitudes where wind can be significantly different, and thus flight direction. However, a reliable estimate of the migratory intensity requires a representative sample of flight directions.

The procedure presented here to quantify bird migration can in principle be applied to any other radar system, provided that the radar is calibrated. Even small ship radars can be operated in a fixed beam mode, which would allow to gather echo signatures, and thus to distinguish between birds and insects. Until now environmental impact studies carried out with ship radars were only based on counting blips on the radar screen and did not consider echo identification and variation of echo size composition with distance and aspect. We hope that our method will improve future radar studies in the scientific and applied research.

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Table 1. Critical points for the quantification of radar targets. See text for futher explanations.

Level	**Crucial points**		**Consequences**	**Effect on results**
echo detection	calibration of echo intensity and STC-effect		unknown loss of echoes	absolute and relative figures unreliable
echo identification	bird → ← insect identification		unknown proportion of birds	absolute and relative figures unreliable; deviation from real bird density depends on insect occurrence
quantification	detection range	mean detection range: weighted by frequency of echo sizes	surveyed space too large or small	absolute figure is wrong; relative comparison possible, if echo sizes are uniformly distributed, otherwise even relative comparisons are wrong
		aspect	surveyed space too large or small	absolute figure is wrong; altitude distribution biased
		detection ranges for bird classes	variability in the composition of bird migration ignored	absolute and relative figure biased due to variation in species composition
	migration traffic rate	flight direction	surveyed range overestimated	absolute and relative figure biased according to the amount of variability in flight directions (e.g. between altitudes and/or nights)
	density	ground speed	inaccurate transformation from MTR to density	absolute figure is wrong; mistake depends on variation of ground speed (mainly wind conditions)

Table 2. Echo parameters that can be obtained from different radar methods. The methods used in this study are marked with asterisks. The brackets indicate that the echo size could not be standardized for all echoes of this methods, because not all of them are detected in the middle of the beam.

radar measurement	echo signature	echo size	air speed	flight direction	distance to radar	representative sample
fixed beam*	**yes**	(yes)	no	no	**yes**	**yes**
horizontal scanning	no	(yes)	**yes**	**yes**	**yes**	**yes**
vertical scanning	no	**yes**	no	no	**yes**	**yes**
conical scanning	no	no	no	no	**yes**	**yes**
tracking*	**yes**	**yes**	**yes**	**yes**	**yes**	no

Table 3. Surveyed volume for wader - (WT), passerine - (PT) and swift types (ST) under low and high elevations. Volumes are divided into sections up to, beyond 3 km and a total value. Total surveyed volume was calculated with a maximum detection range of 7.5 km, compare Fig 5.

	bird class	volume (km^3) up to 3 km	volume (km^3) beyond 3 km	total volume (km^3)
low elevation	WT	0.0225	0.0296	0.052
	PT	0.0224	0.0231	0.046
	ST	0.0279	0.0284	0.056
high elevation	WT	0.0514	0.1406	0.192
	PT	0.0323	0.0552	0.088
	ST	0.0551	0.1609	0.216

Figure 1. Schematic view of how to quantify radar data. The three basic steps are given in separate boxes. Depending on the level of identification the last step (quantification) can be provided separately for different echo groups (e.g. wader -, passerine -, and swift type).

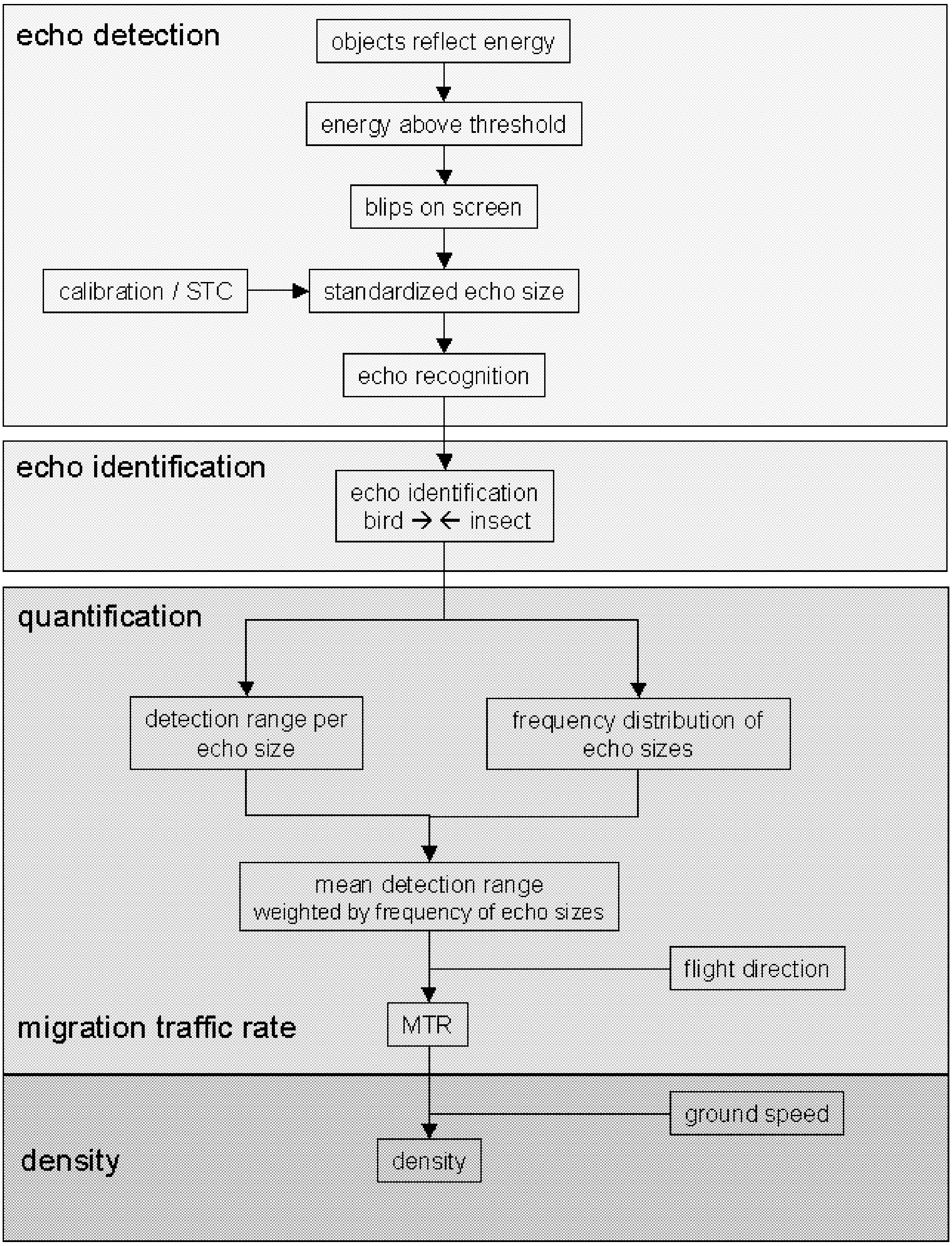


Figure 2. Effect of the STC. The raw radar picture on the top left shows all echoes that have reflected energy above the given threshold including a broad and a small band of clutter at short and many more echoes at far distances. To the right the same picture is shown after applying the STC, comprising only echoes above the given threshold. Echoes being excluded by the STC were clutter and insects. Below the echo signature of a single echo is enlarged. It shows that the echo to the left combines two objects crossing the radar beam, a bird (passerine) and an insect. In the right picture the insect echo did not exceed the STC-threshold and thus, does not appear anymore.

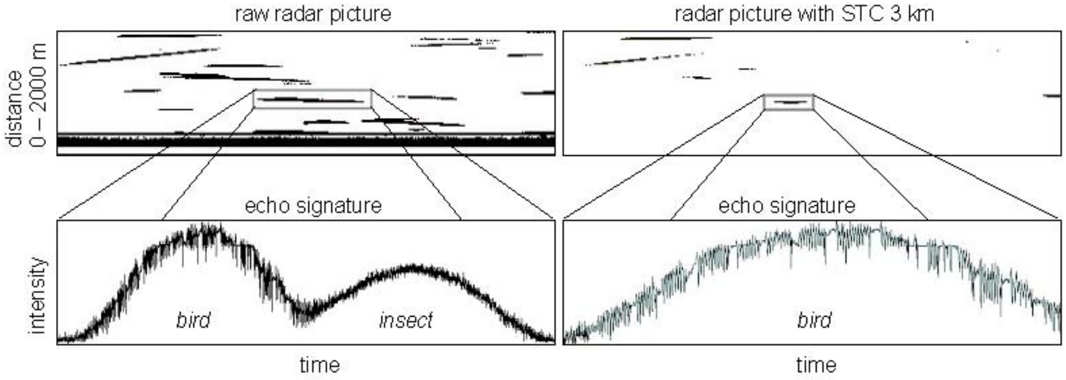


Figure 3. Boxplot of air speed, standardized echo size and standard deviation of echo signature of visually identified insects (lightgrey) and birds (darkgrey) of tracked targets of all seasons. Differences between insects and birds were all highly significant (Mann-Whitney U-test, W = 164 049.5, W = 63 011, W = 424 201, all p-values < 0.0001, respectively), as indicated by the not overlapping notches. Differences in sample size were due to missing values for some tracked targets.

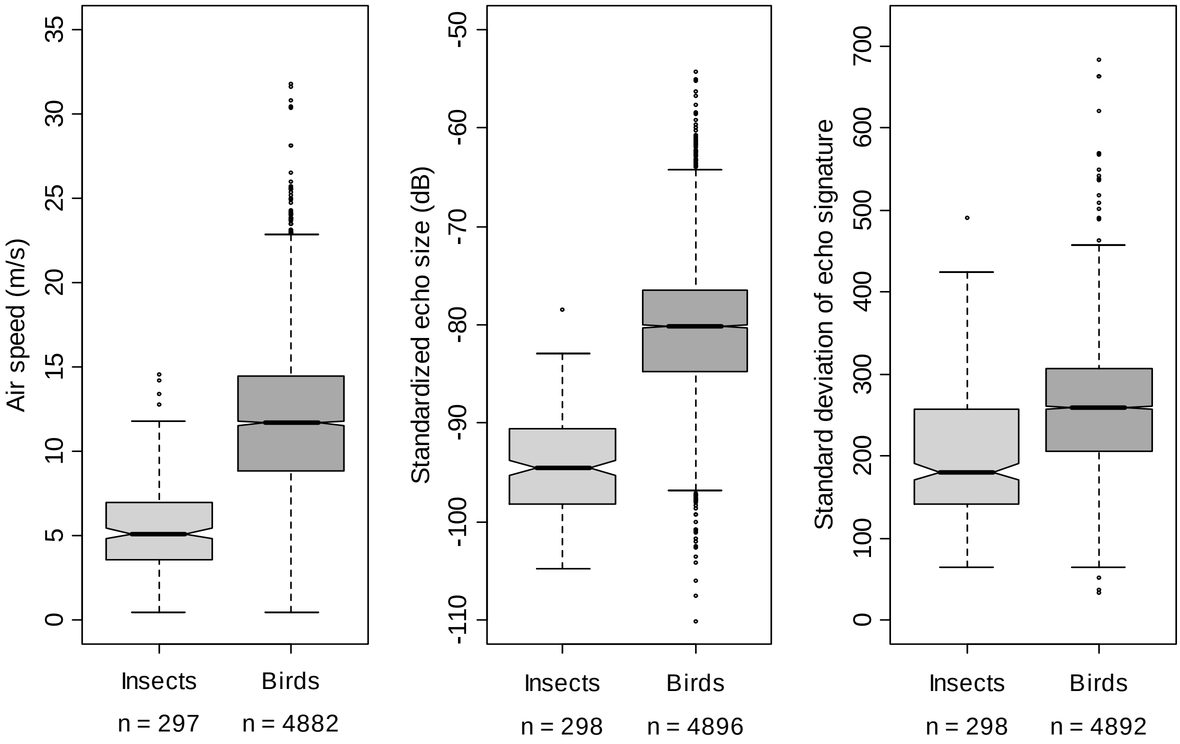


Figure 4. Determination of maximum detection range for bird echoes of fixed beam measurement: standardized echo sizes were plotted over distance and echo size class of -78 dB contained most echoes (n = 1154). Its farthest away echo was taken as a reference value for its maximum detection range (5970 m).

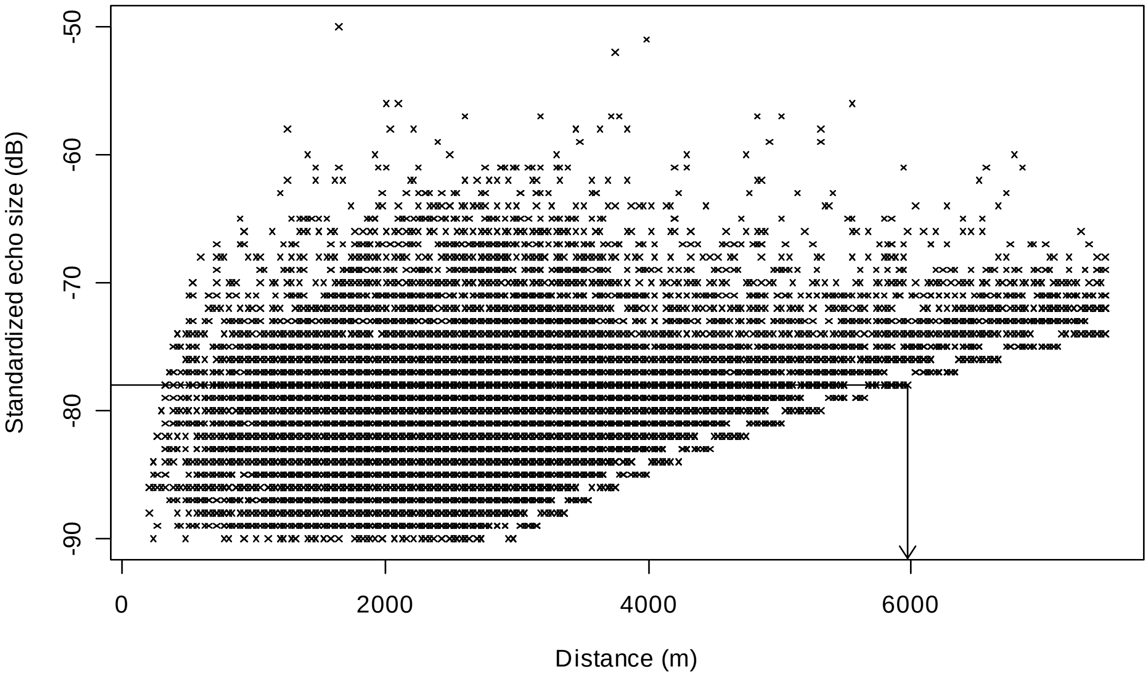


Figure 5. Distribution of standardized echo size of three different bird classes in relation to aspect. Echoes were flying through the beam centre and maximum distance was set to 3 km. Lightgrey boxes indicate low and darkgrey boxes high elevation measurements, respectively. Not overlapping notches reflect highly significant differences between echo size distribution of low and high elevation measurements. Mann-Whitney U-test for a comparison of low and high elevation standardized echo sizes for wader - (WT), swift - (ST) and passerine types (PT) (W = 13 137, W = 3094.5, W = 274 080, all p-values < 0.0001, respectively).

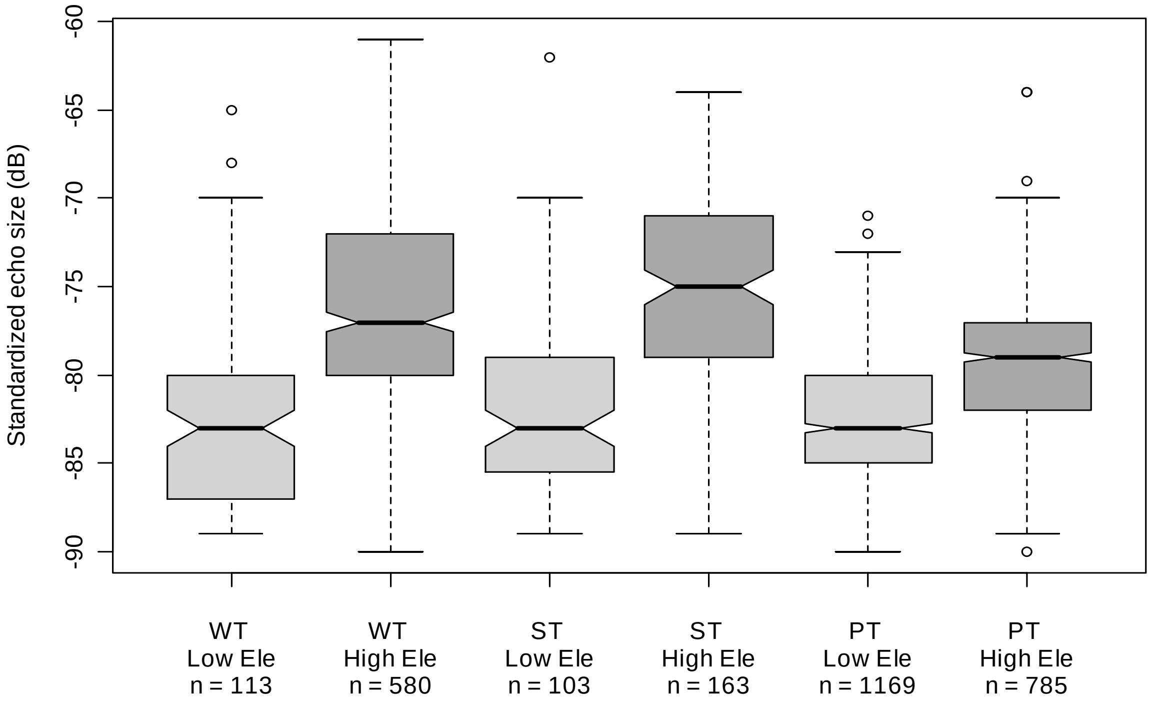


Figure 6. Radar beam as beam width over distance for passerine (solid line) and wader types (dotted lines) of low (narrow lines) and high elevation (broad lines). Calculated radar beam detection for passerine, wader and swift types possessed an opening angle of 3.2°, 3.4° and 3.6° for low elevation and 3.9°, 4.9° and 5.0° for high elevation, respectively. Radar beam for swift types was not included in this figure for the sake of clearness and maximum detection range was restricted to 7.5 km.

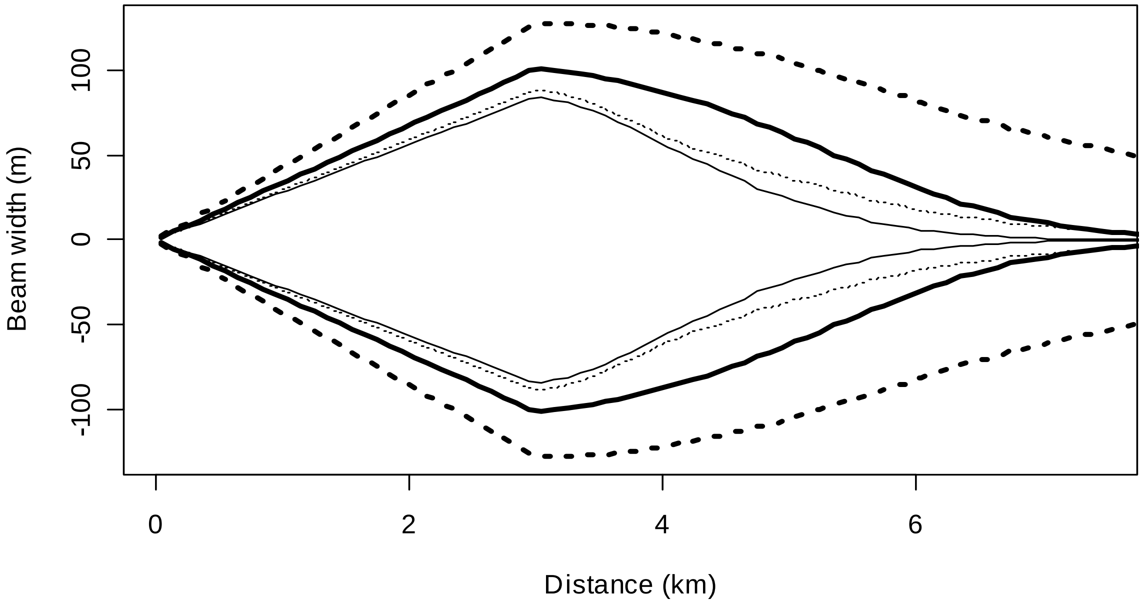


Figure 7. Determination of the sampling units. Dotted line indicates the radar beam, which is widen for the sake of clearness. The narrow solid line describes the trapezium and the broad solid line the initial sampling unit. The actual sampling unit is the projection of the initial sampling unit perpendicular to the birds' flight direction.

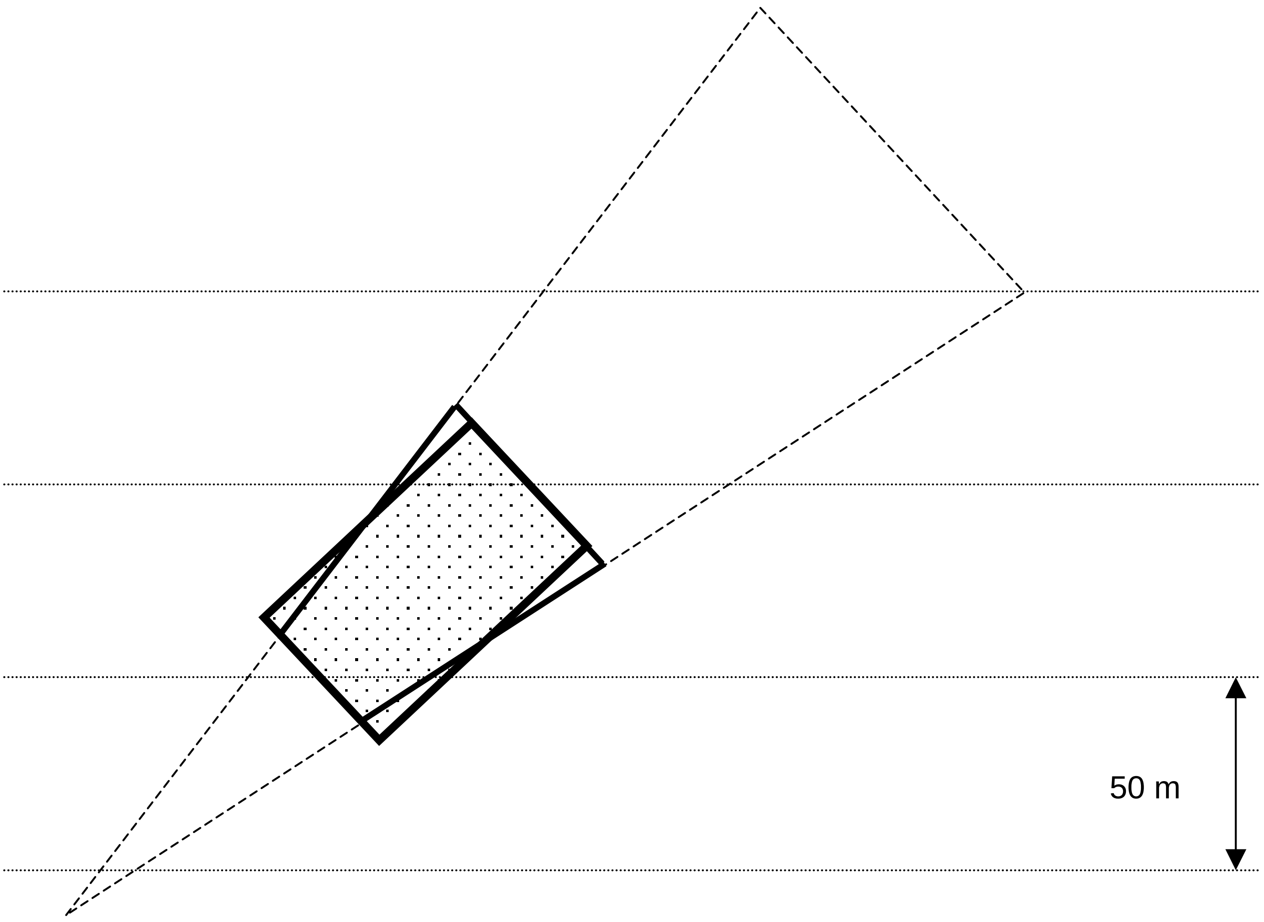
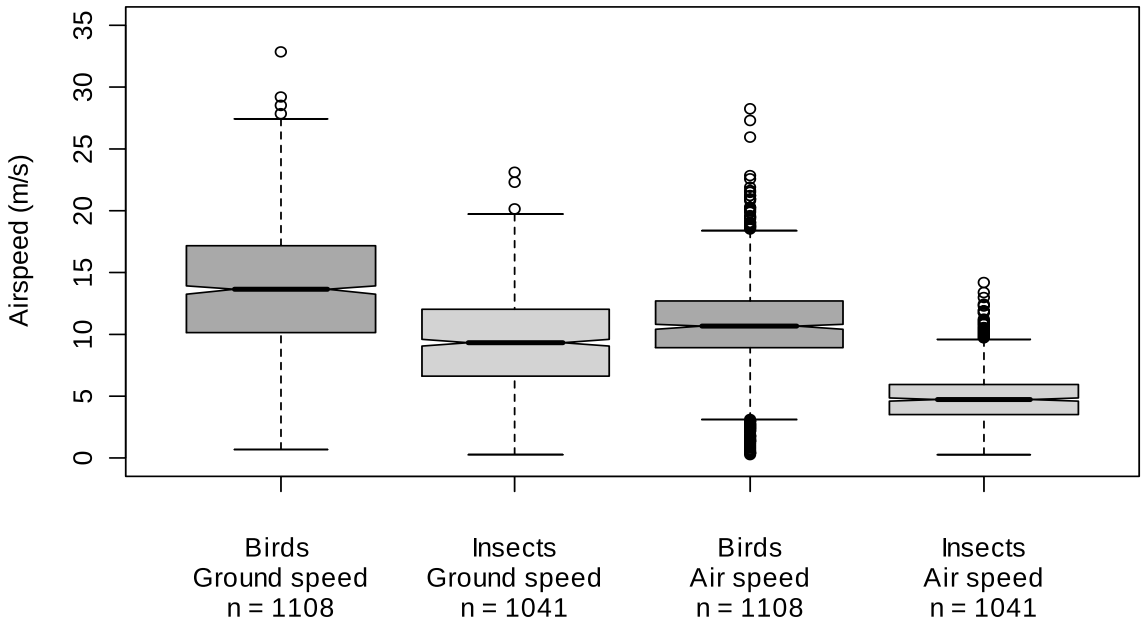


Figure 8. Ground and air speeds of tracked birds (darkgrey) and insects (lightgrey) of all seasons. One-sample Wilcoxon tests of birds ground to air speed and insects ground to air speed and Mann-Whitney U-tests of birds to insects ground and air speed produced highly significant differences (for all p-values < 0.0001), with V = 507 493, V = 525 024, W = 859 470 and W = 1054 271, respectively. Altitude had to be higher than 100 m above ground level, mean vertical distance to wind measurement less than 100 m, time difference to nearest wind measurement less than 1 h, horizontal distance to nearest wind measurement less than 1 km.



III

Daytime passerine migrants over the Sahara – are these diurnal migrants or prolonged flights of nocturnal migrants?

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Passerine migrants are usually divided into diurnal and nocturnal migrants; when crossing the Sahara it was expected that nocturnal migrants would continue their flight into the day. We investigated whether migration taking place in the Sahara during daytime comprises the normal diurnal migrant species or the nocturnal ones prolonging their flight into the day.

Birds departing from the Sahel in spring had to cross an ecological barrier of 300 km before reaching our study site, an oasis in central Mauritania. The intensity of passerine migration measured by radar varied from night to night and decreased towards sunrise. Under good wind conditions some passerine migration continued into the day. Landing tendency (sink rates) correlated negatively with tail wind component. Transect counts on the ground revealed very low proportions of diurnal migrants, not going along with the relatively high densities of passerine migration during the day, and the high correlation between transect density of nocturnal migrants and nocturnal passage of passerine migrants. Therefore we conclude that nocturnal passerine migrants are responsible for most of the recorded daytime passage (swifts, swallows and soaring birds being excluded). Flight and landing behaviour varied with environmental conditions and nocturnal passerine migrants adjusted their flight schedules opportunistically, continuing into the day in particularly favourable winds.

Keywords: bird migration; passerine; Sahara; nocturnal migration; radar

Introduction

Passerines breeding in Europe and wintering south of the Sahara can be divided into diurnal and nocturnal migrants. Swallows (Hirundinidae), larks (Alaudidae), wagtails and pipits (Motacillidae) and to a smaller extent also Ortolan Buntings (*Emberiza hortulana*) fly mostly during the day [diurnal migrants hereafter] (Dorka 1966; Alerstam 1990 and Winkler 1999). Departure may be up to half an hour before sunrise, but passage is most intensive during the earliest hours of the morning and decreases towards midday. In some species a second peak occurs occasionally in the evening (Gehring 1963; Alerstam 1990). All other passerine trans-Sahara migrants are nocturnal migrants, such as thrushes (Turdidae), warblers (Sylvidae) and flycatchers (Muscicapidae) [nocturnal migrants hereafter] (Dorka 1966; Alerstam 1990 and Winkler 1999). They show intensive take-off just after sunset (Alerstam 1990; Bruderer & Liechti 1995; Åkesson *et al.* 1996), while migration fades out towards sunrise. A radar study in the semi desert of the Negev (Israel) revealed a clear gap between night- and daytime migration with nearly no passerines continuing flights at dusk and dawn (Bruderer & Liechti 1995), but compare Gauthreaux (1978) and Bingman (1980).

However, this strict separation is weakened by species prolonging their migration into day or night when crossing ecological barriers, such as oceans (Snow 1953; Williams & Williams 1978; Spina & Pilastro 1999), for reviews see Gauthreaux (1978) and Martin (1990). The Sahara represents an ecological barrier due to heat during day and only few oases serving as sites for refuelling or resting (Moreau 1972). Whether diurnal or nocturnal migrants change their migratory strategy when crossing this desert is unknown. After Moreau (1961), Curry-Lindahl (1981), Lövei (1989) and Biebach *et al.* (1986) non-stop migration is favoured by nocturnal migrants or is at least a commonly used strategy (Biebach *et al.* 2000). An intermittent strategy for the Sahara crossing is suggested by Bairlein (1985, 1988), Carmi *et al.* (1992) and Biebach *et al.* (2000). Bruderer (1994) and Bruderer & Liechti (1995) could demonstrate that passerine migration was restricted to nighttime in the semi desert of the Negev in Israel. However, nocturnal migrants may prolong migration into the day when flying under good wind condition (Gauthreaux 1971). See also Biebach *et al.* (2000) for a summary of this controversial discussion.

To find out whether movements of nocturnal migrants are restricted to nighttime, we carried out a radar study combined with ground observations in Mauritania during spring migration 2003. The study site, the more or less isolated oasis Ouadâne, lies about 500 km east of the Atlantic coast and 300 km north of the Sahel zone. Along the main approach direction of the migrants, which is from SSW (tracks) or S (headings), there is mainly open desert with only sparse and scattered vegetation; the next large vegetation area is the Sahel.

With the aim in view that we will later study the relative importance of non-stop and intermittent migration, we have in a first step to clarify, whether daytime passage of passerine migrants at Ouadâne consists of real diurnal migrants or of nocturnal migrants prolonging their flights into the day.

Material and Method

The study site in Ouadâne was 426 m above sea level (20°56'0.3'' N; 11°35'35.4'' W). The radar was operated from 06 March to 15 May 2003 with a daily break of 2 hours alternating daily from 12h to 14h, 14h to 16h and 16h to 18h, respectively. For information on the radar methods used, see Bruderer (1994) and Bruderer *et al.* (1995a). Quantitative data on the density and altitudinal distribution of migration were recorded every half-hour from 19h to 09h and every hour from 09h to 19h, for further detail see Liechti and Schmaljohann (this volume), (Bruderer *et al.* 1995a). Wind measurements were conducted every day at 07h, 19h and 23h up to 4 km above ground level. Qualitative data on bird species, flight directions, horizontal and vertical speed were collected by radar tracking between quantitative measurements (Bruderer 1969; Liechti & Bruderer 1995). If possible, tracked birds during daytime were identified visually through a telescope (12.4x, mounted parallel to the optical axis of the radar antenna). The expressions “diurnal migrants” and “nocturnal migrants” are used for species migrating usually to a large extent in daylight and at night, respectively. On the other hand, we use day- and nighttime migration to describe the movement of any species during the corresponding time of day. To study the importance of daytime passage of nocturnal migrants, we had to exclude as far as possible real “diurnal migrants” from our samples. This was achieved by (a) defining the proportion of landed “diurnal migrants” compared to landed “nocturnal migrants” according to transect data; (b) by identifying radar targets according to their echo signature as passerines or non-passerines; (c) by excluding Hirundinidae from the calculated diurnal passerine densities (according to their proportion within the samples of echo signatures; Bruderer *et al.* 2001 and Liechti & Bruderer 2002) or by visual identification. Similarly, Apodidae and Meropidae could be excluded from the analysis. Large soaring birds could easily be identified visually over large distances during day or excluded according to their echo signatures.

For the following calculations, we first defined the proportion of birds with recognizable passerine-type wing-beat pattern (excluding Hirundinidae, Apodidae, Meropidae, soaring birds, as well as all flocks of birds) and calculated the passerine density for four altitude classes (0-1 km, 1-2 km, 2-3 km, 3-4 km) in seven time periods of two hours as described by (Bruderer & Liechti 1999):

$$\frac{\text{number of tracked passerine}}{\text{number of tracked echoes}} \times \frac{\text{density of echoes}}{\text{km}^3}$$

Based on wind speed and direction at the birds flight altitude, heading and air speed was calculated; for further details see Bruderer (1971) and Bruderer *et al.* (1995a).

Time classification for the present study started at midnight (00h) and enclosed 7 periods of two hours (until 14h). Using the second half of the night and the first half of the day, allowed us to compare “neighbouring” time sequences. Furthermore, we compared a period of the night with already slightly reduced densities with the most intensive phase of daytime migration, thus achieving the best level of comparability and excluding the very weak migration in the afternoon with frequent zero values. Occasional short breaks due to radar maintenance caused slight variation of sample sizes between time periods.

Time of sunrise shifted from 07h03 on 06 March to 06h09 on 15 May 2003, so that change from night to day was always within the 4th time period. For this study night migration was defined to last from 0h to 06h [“night” hereafter, excluding the twilight period] and daytime migration from 08h to 14h [“day” hereafter], respectively.

From all passerine tracks per time period and height interval we defined the maximum tailwind component [TWC hereafter] for the individuals experiencing the wind direction closest to 0°. 0° was close to the mean heading of all passerines during all periods considered (358.5°, mean vector length = 0.90, n = 4490, Batschelet 1981). Thus, TWC for a specific interval for a time period *i* is:

$$\text{Best individual TWC}_i = \cos(\text{wind direction - } 0°) \times \text{wind speed.}$$

The TWC_{Wind} available for the birds were determined by using the 07h wind measurement. TWC_{Wind} was calculated as the mean of maximal TWC of the four altitude classes [TWC_{Wind} hereafter]. We used this TWC, because passerines often choose altitudes for migration with the most favourable wind conditions (Bruderer *et al.* 1995b).

To obtain information about the landing tendency of passerines, we chose the median vertical speed of passerines of each time period as a measure of the descending or ascending tendency of the birds. Only time periods with more than 4 passerines were included in this analysis.

A transect count was carried out every morning from 27 March to 14 May 2003 to obtain information on species composition and quantity of landed migrants. The transect was a straight line of about 1000 m in the open *Accacia* and *Balanites* woodland in one part of the oasis. Densities were calculated with DISTANCE 4.1 (Thomas *et al.*

2002), for further information see Roth (2004). Passerines observed during the transect were divided into diurnal and nocturnal migrants following Dorka (1966), Alerstam (1990) and Winkler (1999). Additional data from the same site but another year (2004) with morning and late afternoon transects were consulted to discuss possible arrivals of diurnal migrants throughout the day.

SPSS 12.0 for Windows was used for statistical analyses.

Results

Quantities of landed diurnal and nocturnal migrants provide hints to the proportion of real "diurnal migrants" involved in migration across the study site and thus comprised in total migration detected by radar. In order to test whether ground observations correspond to a certain extent to migration aloft, we tested the daily transect density of nocturnal migrants for dependence on passerine densities of the previous night in the radar samples. Transect density of nocturnal migrants correlated significantly with mean passerine night density in the radar (Pearson correlation: n = 49; $R^P = 0.375$, p = 0.008). For the rare "diurnal migrants" such tests revealed no significant dependence on daytime passerine radar densities (Spearman rank correlation: n = 15, $R^S = -0.300$, p = 0.278). Therefore, the ratio of night- to daytime passerine density detected by radar (0.64 birds*km^{-3} / 0.20 birds*km^{-3} = 3.2) could be compared with the ratio of mean ground densities of nocturnal and diurnal passerine migrants (without swallows) of the line transects (6.14 birds*ha^{-1} / 0.07 birds*ha^{-1} = 86.5). Considering that on the transects "nocturnal migrants" were 98 – 99% more frequent than "diurnal migrants" and no correlation of landed "diurnals" with daytime passerine radar densities was detected, we assume that "diurnals" did not represent an important fraction of the daytime migration observed by radar.

The density of passerine migration increased from the first to the third time period and then decreased (Fig. 1.). Relatively high passerine densities were still observed after the sunrise-period, i.e. in the fifth and sixth time period. Mean night passerine density was 0.64 birds*km^{-3} (S.D. 1.06 birds*km^{-3}, n = 69 days), whereas daytime density of birds identified as passerines averaged at 0.20 birds*km^{-3} (S.D. 0.58 birds*km^{-3}, n = 65 days).

The daytime passerine densities measured by radar varied markedly between days (Fig. 2.). Days with mean densities above average had a significantly higher TWC (n = 23, mean TWC_{5-7} = 4.34 m/s, S.D. 4.42 m/s) than those below average (n = 33, mean TWC_{5-7} = 1.24 m/s, S.D. 5.12 m/s; Mann-Whitney u-test: n = 56, Z = -2.024, p = 0.043).

High passerine densities occurred only in mornings when the birds experienced good TWC (Fig. 3.). Densities never reached the seasonal average under unfavourable TWC. The available TWC_{Wind} (mean = 3.6 m/s, S.D. 4.5 m/s, n = 66) did not differ significantly from chosen TWC of passerines during the fifth time period (mean = 3.3 m/s, S.D. 5.0 m/s, n = 55) (t-Test: p (2-tailed) = 0.960) indicating that passerines chose the altitude with the best available wind for migration.

The vertical speed of passerines and the experienced TWC were positively correlated in the fourth and fifth time period (Spearman rank correlation: n = 42, $R^S = 0.430$, p = 0.004; n = 28, $R^S = 0.477$, p = 0.010, respectively), but neither in time periods before nor afterwards (Fig. 4.). Thus, the landing tendency of passerines was lower under good than under bad TWC around sunrise and afterwards. However, vertical speed was nearly always negative for the majority of cases, indicating a weak overall landing tendency. Mean altitude distribution during morning revealed a high proportion of migrants being still at high flight altitudes, indicating prolonged nocturnal migration (Fig. 5.).

Discussion

Average passerine densities did not decrease abruptly around sunrise, but diminished gradually towards midday (Fig. 1.). Did this daytime passerine migration consist mainly of diurnal migrants or of nocturnal migrants continuing into the morning? As the ratio of nocturnal to diurnal passerines detected on the transect was by an order of magnitude higher than the ratio of night- to daytime passerine migration detected by radar, we conclude that most of the passerines migrating in the morning were nocturnal migrants. However, diurnal migrants could have reached the transect area after the transect. To account for this, we carried out one morning and one afternoon transect at the very same site in 2004. Altogether only 5 diurnal migrants were recorded during mornings and 6 during afternoons, respectively. Thus, the ratio of nocturnal to diurnal migrants did not show a shift towards a predominate occurrence of diurnal migrants on the ground in the afternoons (3133 nocturnal : 5 diurnal migrants during the morning transects and 2628 : 6 during afternoons, respectively).

Furthermore, only 2 diurnal migrants (among 852 first captures) were mist-netted at the ringing site during mornings and afternoons [one Short-toed Lark (*Calandrella brachydactyla*) and one Yellow Wagtail (*Motacilla flava flava*)]. Systematic daytime observations of low-level migration – within the lowest 100 m – by means of binoculars and random surveys around the station did not reveal a higher ratio of diurnal migrants (unpubl. data.). There is no obvious reason why nocturnal migrants use the oasis as a stopover site, while diurnal migrants should avoid it. We therefore assumed that diurnal migrants have been recorded on the ground in nearly the same ratio as they flew over.

The course of nocturnal passerine migration was different from the results of other radar studies. Close to Malaga (southern coast of Spain) there was a steep decrease in the overall migration density around sunrise in spring and autumn (Bruderer & Liechti 1999). However, densities did not abruptly go down to zero and since migrants had to finish their sea crossing, it can be assumed that at least some nocturnal passerines continued migration into the day. Bruderer & Liechti (1995) observed a clear gap between day- and nighttime migration in a semi desert in Israel in spring and autumn. In contrast to the large ecological barrier south of Ouadâne, offering nearly no resting sites for migrants, passerines could find extended dwarf shrub vegetation and various patches with trees and bushes for stopover in the Negev within a few kilometres off the radar site. In the areas dominated by sand deserts south of Ouadâne, feeding is much more difficult. Our observations at Ouadâne suggest that under unfavourable wind conditions, nocturnal migrants over the western Sahara show intermittent migration like those in the Negev, while with favourable winds most of them continue migration into the day.

In the case of sea crossings it is a common feature that nocturnal migrants continue migration to reach land; this was shown by radar studies (Baird & Nisbet 1960, Gauthreaux 1971, review by Williams & Willimas 1990) as well as by catching data (Spina & Pilastro 1999, Grattarola et al. 1999). Based on radar observations, Gauthreaux (1971) suggested that song birds crossing the Gulf of Mexico in spring prolonged their migration under favourable wind conditions into daytime after having reached the coast. However, diurnal and nocturnal migrants could not be distinguished. At an inland study site Bingman (1980) observed visually some prolonged flight activity of nocturnal migrants in to the day. Similarly, Gauthreaux (1978) observed visually that at least some nocturnal migrants fly during the morning to correct for drift suffered during the previous night. Both studies comprise movements of unknown density at low levels and may thus show short distance movements to preferred habitats. In our data no differences could be found neither in heading between night- and daytime migration (mean heading$_{night}$ = 359.3°, mean vector length = 0.92, n = 3805; mean heading$_{day}$ = 353.2°, mean vector length = 0.83, n = 685, respectively) nor in flight direction (mean flight direction$_{night}$ = 8.6°, mean vector length = 0.87, n = 3805; mean flight direction$_{day}$ = 359.6°, mean vector length = 0.77, n = 685, respectively) (Batschelet 1981); thus, there were no compensatory movements. Additionally, the daytime movements in the Sahara were at similar altitudes and comparable to nighttime migration with respect to densities. Therefore, we consider these daytime movements as real migration of mainly nocturnal migrants.

High density passerine migration depending on wind conditions (Fig. B) corresponds to a certain extent to the wind dependence of nocturnal migration observed by Liechti et al. (2000) and Erni et al. (2002) in Europe. Bruderer *et al.* (1995b) found increased proportions of descending birds around dawn, but suggested that the main and final landing phase of nocturnal migrants is very difficult to record because it is often nearly vertical (see Hedenström & Liechti 2001). If migration of nocturnal migrants were limited to nighttime, nocturnal migrants prolonging their migration into the day should land when finding reasonable stopover sites (Bruderer & Liechti 1999). Under this precondition, nocturnal passerines should land when arriving at Ouadâne. The gradual decrease in migratory density from before sunrise (04-06h) to after sunrise (08-10h) indicates that many migrants actually land. Flight altitudes reflect this landing tendency by relatively low heights around sunrise (06-08h). However, after that, the relative height distribution of the passerines remaining in the air (08-10h, 10-12h) is similar to those recorded during the night (Fig. 5.). In general nocturnally migrating passerines still flying after sunrise showed a higher tendency to land when facing bad TWC than birds encountering good TWC. The positive correlation between median vertical speed and TWC for the times of 06-08h and 08-10h, indicates that prolonged migration took mainly place when birds experienced favourable conditions (Fig. 4.). After 12h migratory density decreased drastically. We assume that either the wave of nocturnal passerines having departed from the Sahel has passed through or that all nocturnal migrants had landed. The fact that median vertical speed was generally negative throughout the morning, indicates that the overall tendency to land was higher than the overall tendency to continue migration.

This study proves that daytime migration of passerines observed in the western Sahara consists primarily of prolonged nocturnal passerine migration. After exclusion of aerial hunters and soaring birds the proportion of other diurnal passerine migrants is probably negligible. On 31 out of 65 days the daytime migration density was considerably lower or equal to 0.1 birds*km^{-3}, while on the remaining days values were high above average. This important variation was not observed in nightime migration. In particular, we found no difference between night densities previous to days with above or below average daytime densities (Mann-Whitney u-test: n = 57, Z = -0.602, p = 0.547). The days with low density daytime migration indicate that intermittent migration is an important flight strategy to cross the Sahara. On the other hand, the days with high density migration combined with favourable winds suggest that the birds can opportunistically shift towards prolonged migration according to environmental and body conditions. Furthermore, the pronounced landing tendency of passerines during the morning indicates that they do not show real non-stop migration, but tend to land slowly in the course of the morning. Our results suggest that wind plays an important role in bird migration (Liechti & Bruderer 1998, Liechti 2006) that not only species or populations may use different strategies, but that individuals may have various options between intermittent migration with flights restricted to nighttime, intermittent migration with flights including parts of the day or real non-stop migration, i.e. flexibility is the main strategy.

Forthcoming studies have to show on the one hand the relative importance of non-stop and intermittent migration during Sahara crossing, on the other hand we will have to analyse the reasons for the prevalence of one or the other strategy. Directions for such analyses are given e.g. in (Bairlein 1985, Biebach et al. 1986; Bairlein 1988; Bairlein 1992) suggesting that most migrants landing in the desert are in a rather good condition, thus indicating prevalence of an intermittent strategy. As not only energy, but also water is a rare resource in the desert, it was suggested, that migration should take place at night due to lower temperatures and less water consumption, whereas roosting in shaded areas during the day may be possible in spite of imminent dehydration due to extreme climatic conditions (heat and water deficiency) (Blem 1976; Austin and Miller 1982; Bairlein 1988; Biebach 1990). The continuing controversy on water balance of migrants crossing the Sahara suggests that other factors, such as diurnal air turbulence increasing the energetic costs of flying (Kerlinger and Moore 1989) have also to be studied.

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Fig. 1. Seasonal mean and standard deviation of passerine density are given for the first half of the day over time of day.

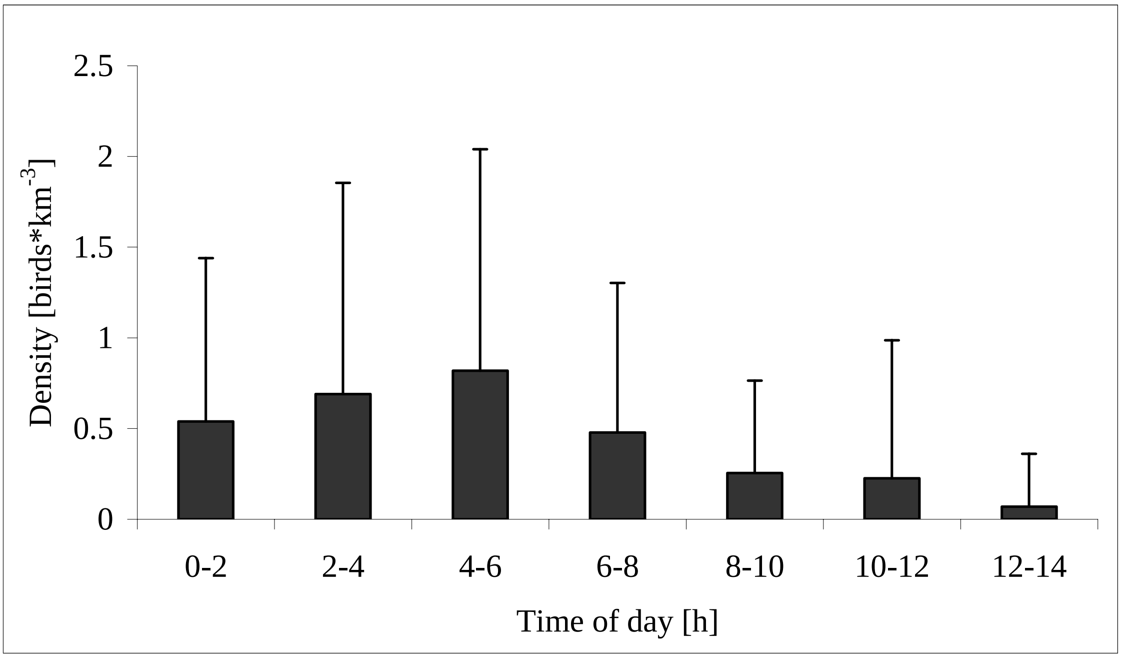


Fig. 2. Mean and standard deviation of daytime passerine density over time of season including hours 08h to 14h, n = 65.

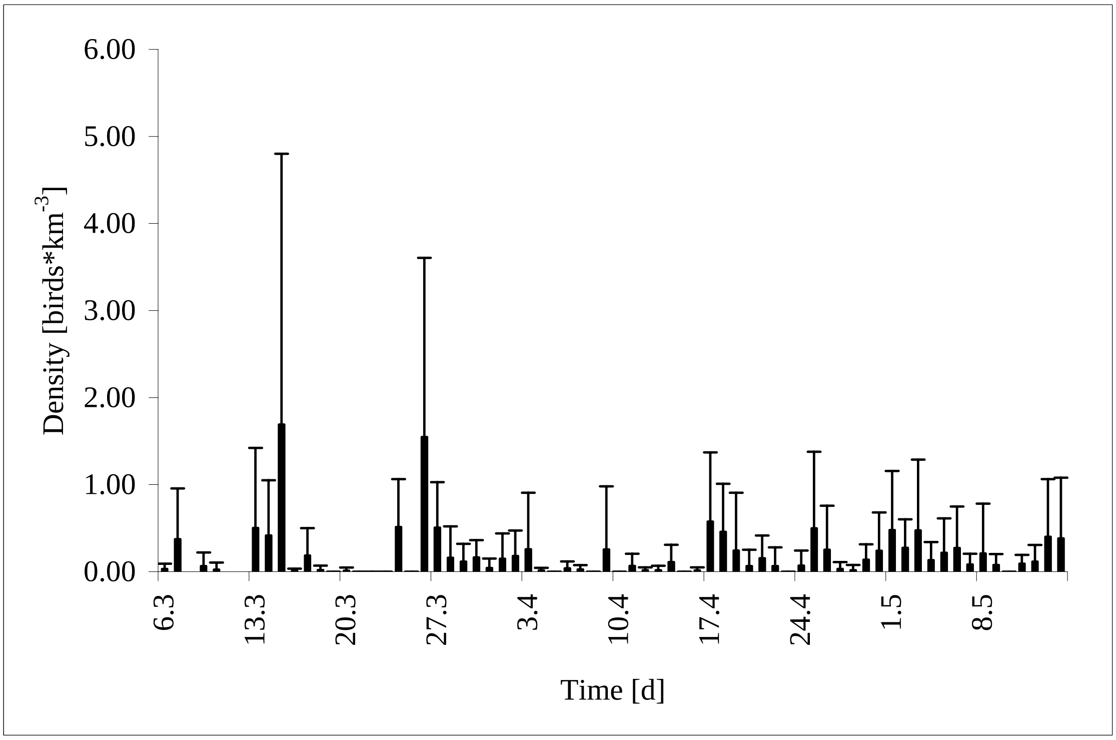


Fig. 3. Passerine density of fifth time period (8h to 10h) over experienced tailwind component of 55 days.

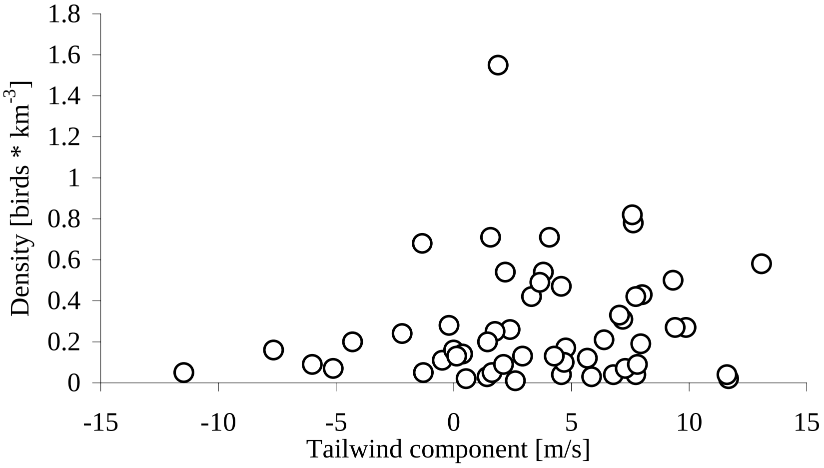


Fig. 4. Median vertical speed of passerines over experienced TWC of fifth time period. Spearman rank correlation: n = 28, R^S = 0.477, p = 0.010.

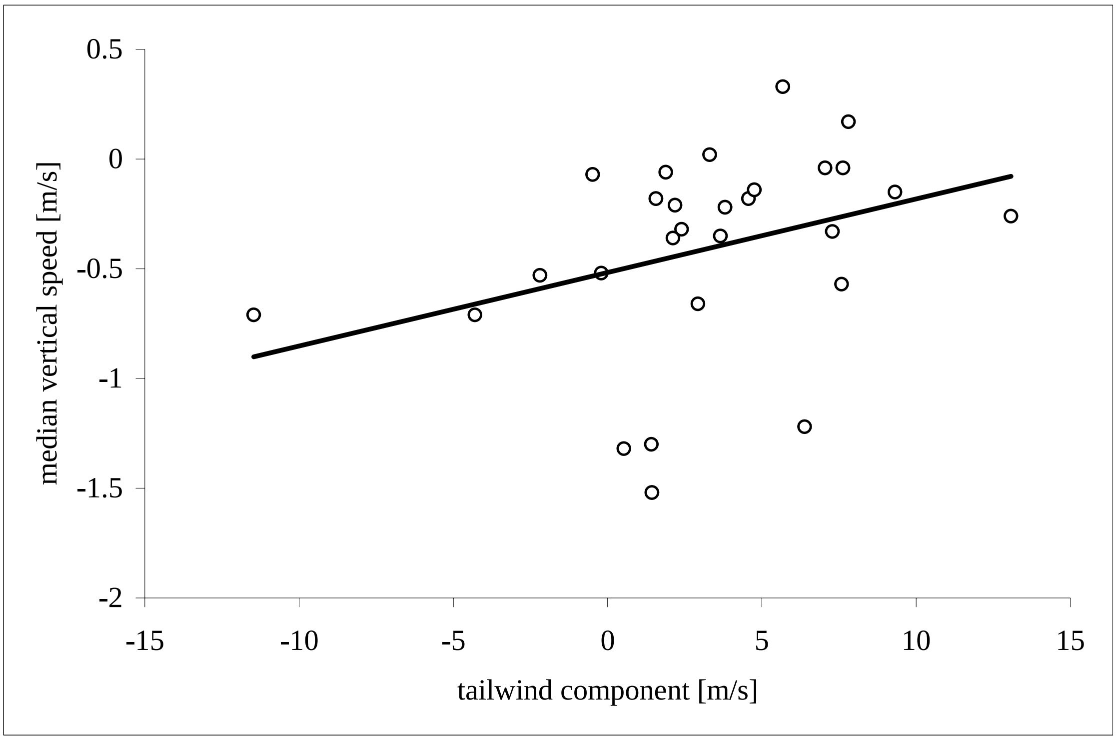
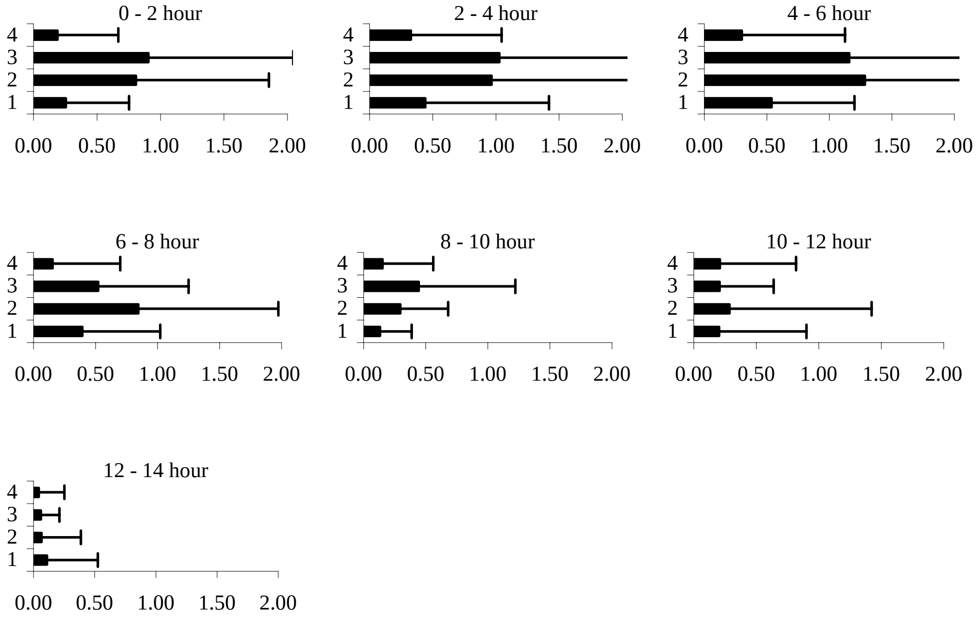


Fig. 5. Mean spring passerine density [birds*km^{-3}] of four altitude classes [0-1 km, 1-2 km, 2-3 km, 3-4 km] in all time periods of two hours from 00h to 14h. Standard deviations are given only to a certain extent.



IV

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Songbird migration across the Sahara: the non-stop hypothesis rejected!

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Billions of songbirds breeding in the Western Palaearctic cross the largest desert of the world, the Sahara, twice a year. While crossing Europe, the vast majority use an intermittent flight strategy, i.e. fly at night and rest or feed during the day. However, it was long assumed that they overcome the Sahara in a 40 h non-stop flight. In this study, we observed bird migration with radar in the plain sand desert of the Western Sahara (Mauritania) during autumn and spring migration and revealed a clear prevalence of intermittent migration. Massive departures of songbirds just after sunset independent of site and season suggests strongly that songbirds spent the day in the plain desert. Thus, most songbirds cross the Sahara predominately by the intermittent flight strategy. Autumn migration took place mainly at low altitudes with high temperatures, its density decreased abruptly before sunrise, followed by very little daytime migration. Migration was highly restricted to night-time and matched perfectly the intermittent flight strategy. However, in spring, when migratory flights occurred at much higher altitudes than in autumn, in cool air, about 17% of the songbird migration occurred during the day. This suggests that flying in high temperatures and turbulent air, as is the case in autumn, may lead to an increase in water and/or energy loss and may prevent songbirds from prolonged flights into the day.

Keywords: bird migration; desert crossing; non-stop migration; passerine; water stress

1. INTRODUCTION

The Palaearctic–African bird migration system comprises nearly four billion songbirds (Moreau 1972). Most songbirds carrying out such long-distance movements migrate only nocturnally in Europe (Dorka 1966; Winkler 1989; Bruderer & Liechti 1999) as well as in the semi-desert of Israel (Bruderer 1994; Bruderer & Liechti 1995). Flight costs of flapping flyers are expected to be lower in laminar air layers at night than in turbulent air during the day (Kerlinger & Moore 1989). Additionally, daytime can be used to recover (Schwilch *et al.* 2002; Fuchs *et al.* 2006) and restore energy and water reserves. When crossing the Sahara, they encounter harsh environmental conditions over a distance of about 2000 km. To cope with heat and scarcity of food and water, they store fat and protein in anticipation (Fry *et al.* 1970; Piersma 1990; Biebach 1998; Jenni & Jenni-Eiermann 1998; Klaassen *et al.* 2000). Therefore, it was long hypothesized that songbirds should cross the Sahara by a long non-stop flight and not waste water and energy by resting during the day in the hot and dry sand desert (Moreau 1961; see also Biebach 1990). Birds occasionally observed in the desert were considered as fallouts. However, the few songbirds captured in the desert were in good body condition and continued their migration after sunset, suggesting an intermittent flight strategy in at least some species or individuals (Bairlein 1985; Biebach *et al.* 1986; Bairlein 1988). Since the temporal and spatial patterns of songbird migration across the desert were never quantified, the question of how many songbirds overcome the Sahara by an intermittent or a non-stop flight of 40 h remained unanswered. Migration models (Carmi *et al.* 1992; Klaassen 1995) and wind tunnel experiments (Engel 2005) revealed some evidence that due to the extreme environmental conditions songbirds flight time might be restricted by water consumption.

We quantified for the first time, to our knowledge, spring and autumn songbird passage in the Western Sahara, Mauritania, by carrying out extensive radar studies at an oasis and two additional sites surrounded by at least 300 km of nearly vegetationless desert. According to the non-stop hypothesis, songbirds, which find themselves after a nocturnal flight at sunrise over the open desert, should continue their flight across the desert. However, songbirds having not yet reached the open desert until dawn are supposed to land before sunrise, as they do in Europe and Israel (Bruderer 1994; Bruderer & Liechti 1995, 1999). Thus, recording non-stop migration at a given site in the desert, we would not expect a continuous flow of migrants throughout the day, but a limited passage of birds for a time period corresponding to the length of a night. Considering non-stop migration, we expected a wave of songbird migrants passing our study sites, timed in relation to the distance to the southern or northern edge of the desert, i.e. the Sahel savannah and the Atlas Mountains, respectively. Assuming that the departure from these last refuelling areas occurred at dusk, which is a general pattern for migrants in North America, Europe and Israel (Gauthreaux 1971; Hebrard 1971; Alerstam 1990; Bruderer 1994; Bruderer & Liechti 1995, 1999; Åkesson *et al.* 1996; Moore & Aborn 1996; Bolshakov & Chernetsov 2004), we calculated for each radar site and season an expected period of passage, based on the averaged measured ground speeds (50 km h^{-1}, see §2). Thus, according to the non-stop hypothesis, the temporal pattern of the passage should differ between the sites according to their different distances from the

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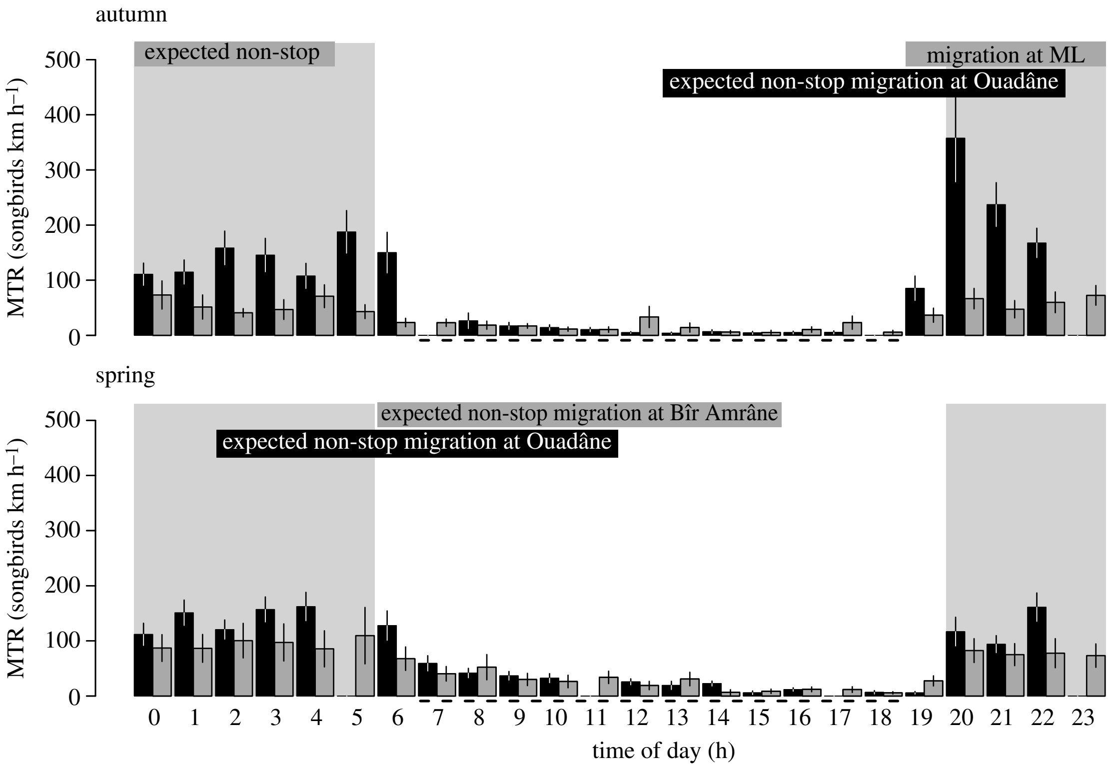

Figure 1. Migration traffic rate (MTR) of songbirds (mean ± s.e.) in the course of the day in autumn and spring, at the constant site Ouadâne (oasis, $n_{\text{autumn}}=63$ days, $n_{\text{spring}}=57$ days; black bars) and two temporal sites (grey bars) in the plain sand desert, Mohammed Lemna (ML) in autumn ($n=12$ days) and Bîr Amrâne in spring ($n=23$ days). The shaded area marks the measurements considered for the nocturnal migration and the dashed line (below x-axis) those for diurnal migration. The horizontal bars indicate the time periods at which the hypothetical non-stop waves of songbirds are supposed to fly over the study sites. The times are calculated based on the distances to the next major departure sites (the Atlas Mountains and Sahel Savannah) and an average ground speed of 50 km h^{-1} (cf. figure 2). Missing bars at Ouadâne are due to lacking measurements.

departure sites, while the intermittent hypothesis would lead to an identical pattern at all sites, with take-off at dusk and landing at dawn (figure 1).

2. MATERIAL AND METHODS

Data were collected in Mauritania close to the oasis Ouadâne, located about 500 km east of the Atlantic coast (20°56′ N, 11°35′ W), in autumn (24 August–25 October 2003) and spring (15 March–10 May 2004), and at two sites (Mohammed Lemna, 18°35′ N, 08°38′ W; Bîr Amrâne, 22°47′ N, 08°43′ W) 300 km further east in the plain sand desert in autumn (19–30 September 2003) and in spring (03–25 April 2004), respectively (figure 2).

To quantify bird migration, a fixed beam method similar to the one suggested by Bruderer (1971) was used, but with a fully computerized recording system. At Ouadâne, fixed beam measurements were carried out at a low and high elevation angle (11° and 79°) every hour and at the other two sites at three different elevation angles three times per hour (Mohammed Lemna, 8°, 28° and 79°; Bîr Amrâne, 6°, 28°, 79°). In doing so, high and low altitudes were surveyed with nearly the same effort. The resulting number of fixed beam measurements for autumn was 2680 in Ouadâne and 2064 at Mohammed Lemna; for spring, it was 2050 in Ouadâne and 3971 at Bîr Amrâne. The beam was directed towards the west (270°) and thus perpendicular to the main migration direction (Schmaljohann *et al.* in press). South of the Ouadâne site was a small vegetation strip within the sandy desert, whereas to the north the rocky desert extended for several hundred kilometres. Therefore, only spring departure data might be directly influenced by the oasis close by. The two desert sites were separated from the next oasis by several hundred kilometres of plain sand desert. The recording time was 4 min and the detection range for songbirds was restricted to about 7 km (Schmaljohann, unpublished data). This system collection of the echo signature of each target crossing the beam and distinguished between birds and insects on the basis of their echo signatures. This identification was essential as insect echoes made up a substantial proportion of all echoes. To quantify songbird passage, we selected only songbirds out of all the detected birds according to their echo signature, i.e. wing beat pattern (Bruderer 1969). Swallows and corvids differ in migration strategy (being diurnal migrants) and flight type (resulting in special wing beat patterns) from the majority of passerines, i.e. Motacillidae, Turdidae, Sylvidae and others, and were excluded from the samples accordingly. For further information about the use of radar for ornithological purposes see Bruderer (1997). Songbirds migrating in the desert during the day may be either nocturnal migrants prolonging their flights or diurnal migrants; in the Sahara, the daytime migration consisted mainly of diurnally migrating nocturnal migrants (Schmaljohann *et al.* in press).

To estimate the time the songbirds would need to cover the distance from the major departure areas to the study sites, we determined their average ground speed at Ouadâne. Single songbirds were tracked by radar and their ground speeds were recorded. Average ground speed was 15.3 ± 5.0 m s^{-1} ($n_{\text{autumn}+\text{spring}}=6485$), which we simplified to 50 km h^{-1}.

The night was defined to last from 20.00 to 05.00 and day from 07.00 to 18.00, because civil twilight occurred during the sixth and the nineteenth hour of the day throughout all the

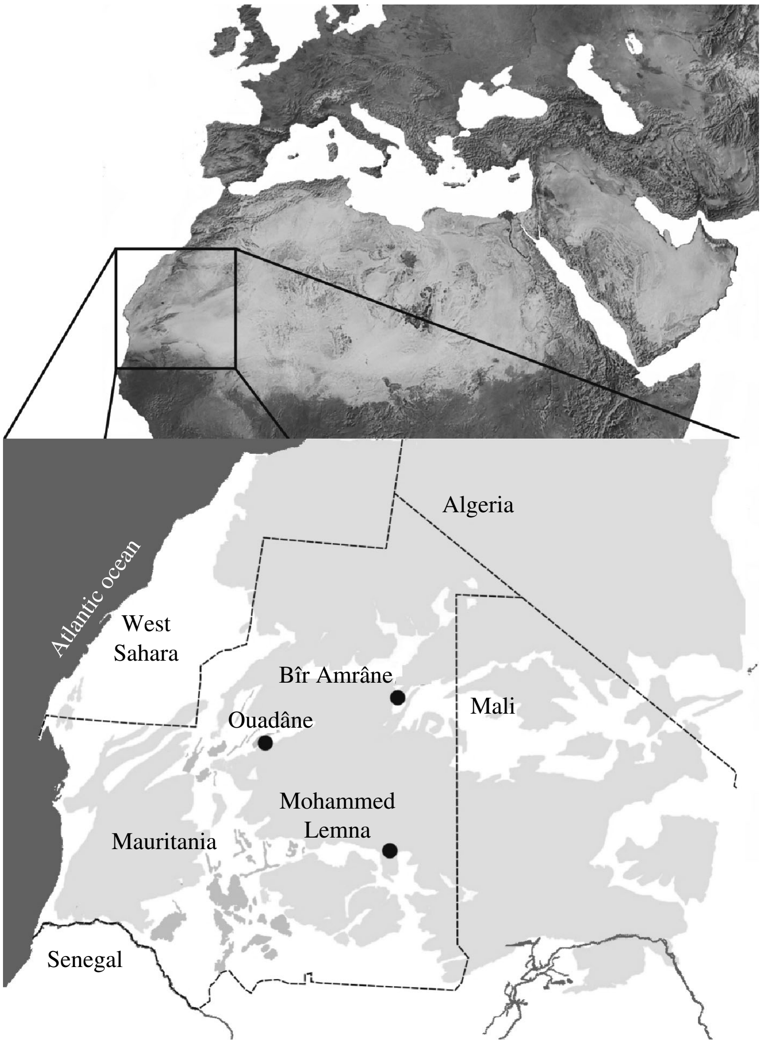

Figure 2. Location of the study sites in Mauritania. The upper map provides an overview of the Sahara with the general location of the studied areas (rectangle), expanded below. In the lower graph, the three study sites are given, whereas the oasis of Ouadâne is situated at the transition from the sandy desert to a stony plateau, Bîr Amrâne and Mohammed Lemna are within the plain sand desert.

study periods. Statistics were calculated using the statistical software package R (R Development Core Team 2005).

3. RESULTS

At all sites, songbird migration intensity increased immediately after sunset, remained relatively high during the night and decreased smoothly after sunrise in spring but abruptly in autumn, especially at the oasis (figure 1). The proportion of diurnal migration (figure 1) at the oasis was significantly lower in autumn (5%) than in spring (17%; Mann–Whitney test, two-tailed, $n_{\text{autumn}}=62$ days, $n_{\text{spring}}=55$ days, $W=2401$, $p<0.0001$). In both seasons and at all sites, migration intensity was very low during the afternoons (from 13.00 to 20.00; Ouadâne autumn, 1.6%; Ouadâne spring, 7.7%; Mohammed Lemna autumn, 6.2%; Bîr Amrâne spring, 4.7%).

4. DISCUSSION

In spring, the last major stopover site before the desert crossing is the Sahel savannah. Any bird taking-off from there and flying non-stop would reach Ouadâne at the earliest at 02.00. The last birds of such a non-stop wave would pass the oasis at around 11.00. This hypothetical non-stop wave would then reach the desert site (Bîr Amrâne), about 200 km further north, 4 h later (average songbird ground speed was about 50 km h^{-1}; figure 2). In autumn, major departure areas are within the Atlas Mountains. First songbirds taking-off there would be expected to reach Ouadâne around midday, and last birds of the non-stop wave should have passed the oasis by 22.00. Owing to the more southern and more inland location of Mohammed Lemna (about 270 km), we assumed that the hypothetical non-stop wave would fly over this site from 19.00 to 04.00. Apparently, the diurnal pattern of songbird migration did not match these expected patterns of the non-stop hypotheses. The massive departure of songbirds after sunset and the persistent migration through the night, independent of site and season, indicate clearly that take-off took place in the vicinity of the study sites and, thus, songbirds rested in the desert during the day (figures 1 and 2). Therefore, the data give strong evidence that intermittent migration is the predominate strategy of songbirds to cross at least the Western Sahara. This confirms the suggestion of Bairlein (1985, 1988), Biebach *et al.* (1986) and Biebach (1990), who concluded from capturing data that at least some songbirds cross the desert intermittently. Taking the four billion songbirds crossing the Sahara in autumn (Moreau 1972) and distributing them evenly in time (90 days) and space (11 000 000 km^2), we would expect to find each day about four birds per kilometre squared. At Mohammed Lemna, a line transect count (1500 m) in the sand desert with a few tiny bushes was carried out daily in the mornings during the study period. At three out of ten transect counts a single subalpine warbler (*Sylvia cantillans*) was observed. When the few small bushes in an area of 200 × 20 m at Bîr Amrâne were searched intensively for birds on 13 out of 19 days, passerine migrants were found; the average number was 5 ± 4 (s.d.) songbirds and the most common species were willow warbler (*Phylloscopus trochilus*, $n=19$), common whitethroat (*Sylvia communis*, $n=18$) and melodious warbler (*Hippolais polyglotta*, $n=12$). Thus, passerines were encountered regularly in the Sahara, although finding them remained hard.

In contrast to autumn, when migration was highly restricted to night-time, passerines prolonged their migratory flights far into the day in spring (figure 1.), but the amount varied extremely from day to day. There is strong evidence from preliminary work, analysing data from Ouadâne 2003 (Schmaljohann *et al.* in press), that this occasional daytime migration, consisting mainly of nocturnal migrants continuing their migration, occurred only under good tailwind conditions. We therefore conclude that passerines prolong their migratory flights opportunistically, depending on the wind conditions during the morning. A slight proportion of songbirds extended migration into the day also at Mohammed Lemna during autumn, where, according to the non-stop hypothesis, no migration should occur before 19.00 (figure 1). Therefore, prolongation of migratory flights into the day seems to be a common pattern in songbirds crossing the Sahara, probably influenced strongly by actual environmental conditions (see below and Schmaljohann *et al.* in press). Such prolongations were also observed in garden warblers (*Sylvia borin*) when crossing the Mediterranean Sea (Grattarola *et al.* 1999) and in other nocturnal migrants when crossing the open sea (Williams & Williams 1978; Spina & Pilastro 1999; for reviews, see Gauthreaux 1978 and Martin 1990). Nevertheless, if the daytime passage in spring was formed by a common wave of non-stop migration, we would expect a time lag between the wave at Ouadâne and Bîr Amrâne of about 4 h. However, there is no evidence for such a difference between the sites, and daytime migration was not recorded everyday. Thus, there is no strong support for non-stop migration, but we cannot fully rule out that some passerines might migrate non-stop.

Although we could point out that most passerines do not cross the Sahara in a non-stop flight, most of them do so in the sense of nutritional terms. Passerines resting in the open desert still migrate ‘non-stop’, because they do not feed during the daytime stopovers. Thus, for passerines, it still remains necessary to intensively refuel before crossing such barriers, as shown, e.g., in northern Africa by Odum (1963) and Bairlein (1988). Hence, our findings are in line with the notion that land birds achieve a maximum departure fuel load just before barrier crossings (Marsh 1983; Dierschke *et al.* 2005).

What might be the reasons that nocturnal migrants prolong their flight into the day regularly in spring, but rarely in autumn? Wind tunnel experiments have shown that under desert conditions flying birds have a negative water budget (reviewed by Kvist 2001; Engel 2005). Red knots (*Calidris canutus*) showed a net water loss with temperatures higher than 20°C (Kvist 2001), whereas flying rose-coloured starlings (*Sturnus roseus*) always possessed a net water loss independent of ambient temperature (Engel 2005). Moreover, flight time was limited by high temperatures (27°C) to 4.5 h in European starlings (*Sturnus vulgaris*; Engel 2005). Nevertheless, temperature did not markedly influence the selection of flight altitudes by nocturnal migrants (Liechti *et al.* 2000; Liechti 2006). Accordingly, in spring, passerine migration in this study was mainly concentrated within the anti-trades (tailwinds for spring migrants) at a height of 2–4 km above ground level. The cool (around 10°C) and relative humid (about 40%) air may result in a relatively low water loss (Carmi *et al.* 1992). In autumn, most birds flew below 1 km above ground level in the trade wind zone (tailwinds for autumn migrants), where temperatures are high (25–35°C) and humidity is low (about 30%; our unpublished data). Hence, water loss is expected to be much higher in autumn than in spring. We therefore assume that spring migrants flying at high altitudes occasionally prolong flight into the day (Schmaljohann *et al.* in press), while autumn migrants flying at low altitudes are restrained by the high diurnal flight costs (water and/or energy). Similarly, water loss might be responsible for the difference in nocturnal flight activity between spring and autumn in the Negev desert (Bruderer & Liechti 1995). In the Negev, migrants did not prolong their flight into the day either in spring or in autumn, but in spring nocturnal flight activity lasted for the whole night, while in autumn it ceased early during the second half of the night.

In general, flight duration of songbirds under desert conditions might be limited either due to the excessive water loss by flying in the blazing sun and through hot and dry air or due to the excessive energy loss by flying in turbulent air during the day instead of in laminar air flow at night (Kerlinger & Moore 1989; Carmi *et al.* 1992; Engel 2005). Therefore, resting on the ground would reduce expenditure of water and/or energy compared with flying with extra costs in daytime. We suggest that the relative advantages of nocturnal flights prevent most songbirds from performing non-stop flights across the Sahara.

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V

Flight altitudes of nocturnal spring migrants over the Sahara governed by wind

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Flight costs make up a large proportion of energy expenditure during migration, and are strongly dependent on atmospheric conditions aloft. Birds crossing the Sahara can take advantage of the fairly reliable trade wind regime. In our study, we investigated whether birds adapt flight altitude to minimise energy or water loss. Data from free flying birds were collected during spring migration with a tracking radar in an oasis in Mauritania, about 500km east of the Atlantic coast. Density measurements revealed the height distribution of the ongoing migration up to 4 km above ground level (agl). Daily radio sondes provided information on temperature, humidity, pressure and wind profiles up to 4 km agl. We compared height distributions of nocturnal migrants with predictions based on the atmospheric conditions. The two models used predicted maximum flight ranges and maximum flight durations either for energy or water constrained birds. Nocturnal migrants were flying mainly 2 km agl, where predicted maximum flight ranges were generally largest. There was little difference between the two models, whereas both models were strongly shaped by the tailwind component. In addition, altitudes, where water loss per flight time was minimal, could explain some of the remaining variance. The results confirm that wind is the most important factor determining flight altitudes in bird migration and, at least in spring, water stress above the desert seems to play a minor role.

Keywords: passerine migration; Sahara; energy and water flight costs; altitude

Introduction

Migrants crossing the Sahara cover large distances between their wintering grounds and breeding sites. Flight costs are considered one of the most import factors shaping the migratory strategies with respect to time as well as to energy optimisation (Alerstam & Lindström 1990). To cross large ecological barriers such as the Sahara desert in a single stage requires large energy reserves, as refuelling sites are very scarce (Bairlein 1985, Biebach *et al.* 1986). However, as pointed out by Carmi *et al.* (1992) water might also be the limiting factor for desert crossing. Carmi *et al.* (1992) developed a model to predict maximum flight ranges with respect to energy and water loss, according to the birds premigratory condition, its flight capacity and the atmospheric situation. This model suggests that dehydration rather than energy will limit flight range and that due to a decrease in oxygen partial pressure with altitude (causing increased respiratory ventilation), birds should fly at levels below 1000 m to cross the Sahara successfully. While Carmi *et al.* (1992) neglected wind influence, Klaassen (1996) enhanced the model by (1) energy constraints including wind influence (after Pennycuick 1989) and (2) water constraints including wind influence. Flight costs and water consumption are expected to vary substantially according to flight altitude, due to the varying atmospheric conditions (Pennycuick 1989, Klaassen *et al.* 1999).

Analysis of radar data from the Gulf of Mexico and southern Israel showed a strong impact of wind on the altitudinal distribution of nocturnal migration (Gauthreaux, Jr. 1991, Bruderer *et al.* 1995b). Analysing altitude distributions of nocturnal spring migrants crossing the semi-arid desert of southern Israel, Liechti *et al.* (2000) found slightly better predictions when water consumption was considered the limiting factor instead of the model considering energy (after Klaassen 1999) alone. For birds crossing the Sahara desert water constraints might be even more pronounced than for those flying across Israel, as temperatures are generally higher, relative humidity is lower and open water is very scarce. A study by Klaassen & Biebach (2000) dealt with height distributions of passerines crossing the Egyptian desert. Their analysis was based on a radar study performed by Biebach et al. (2000), which had significant methodological shortcomings (s. discussion).

For this study we used radar measurements of spring migration in the Sahara desert of Mauritania. Altitudinal distribution of nocturnal migration was compared with predictions based on simultaneously recorded altitudinal profiles of weather variables in the same way as done by Liechti *et al.* (2000). We expected that water constraint should be more accentuated in the Sahara than in Israel. If water was actually a limiting factor, predictions based on water constraint would show a better match with the observations than in Israel.

Methods

Field data

Data on migratory intensity were recorded by a tracking radar "Superfledermaus" at a site close to the oasis of Ouadâne (20°56’0.3’’ N; 11°35’35.4’’ W, 426 m above sea level) in the Mauritanian part of the Sahara desert. The radar was operated from 06 March to 15 May 2003 with a daily break of 2 hours alternating daily between 12 to 14h, 14 to 16h and 16 to 18h, respectively. Quantitative data on the density and altitudinal distribution of migration were recorded every half-hour from 19 to 9h and every hour from 9 to 19h. Wind measurements were conducted every day at 7h and 19h. At 23h a radio sonde was launched and tracked by radar to gather altitudinal profiles of air pressure, temperature, relative humidity and wind. For details on echo density measurements see Bruderer *et al.* (1995a). Echo density was calculated for 200 m height intervals up to 4000 m above ground level (agl). Due to ground clutter the lowest 100m had to be omitted. A mean height distribution for 200 m intervals comprising six measurements (22h00h, 22h30, 23h00,23h30, 0h00, 0h30) was calculated for each night. On some nights there was considerable contamination of the radar data with insect echoes. From tracking single echoes we were able to estimate the proportion of insect echoes (flight levels were mainly below 1000m agl). A few nights with strong insect contamination were excluded. Fifty nights remained for this study, with continuous altitudinal profiles for echo density, wind, temperature, relative humidity and air pressure.

Model predictions

We applied the same model settings as used by Liechti *et al.* (2000), except that body frontal area was calculated after Hedenström and Rosén (2003). As a model bird we used a Willow Warbler (*Phylloscopus trochilus*) in line with settings used by Carmi *et al.* (1992) and Liechti *et al.* (2000). We abstained from applying an additional model with the Golden Oriole (*Oriolus oriolus*) as done by Klaassen & Biebach

(2000) and Liechti et al. (2000), because both analyses showed that differences in the predictions of optimal flight altitudes were negligible. Input data for the Willow Warbler were: body mass 10 g, wing span 0.17 m, wing area 0.0069 m², fuel fraction of initial body mass 0.3, water fraction of initial body mass 0.5 (assuming a water content of the lean tissue of 71%), maximum water loss fraction of initial water content was arbitrarily set to a value of 60%. Fuel reserves were considered to consist of 70% fat, 9% protein and 21% water, resulting in an energy density of 29 kJ/g and a metabolic water yield of 1.00 g per g fuel, (Klaassen 1995, Jenni & Jenni-Eiermann 1998). Flight directions were highly concentrated and almost due North (Schmaljohann *et al.* in press). Thus, for tailwind calculations we choose 0° as the preferred migratory direction. For further details on the model calculations see Liechti *et al.* (2000).

Based on the atmospheric conditions (wind, temperature, rel. humidity, air pressure) the model output provided for each 200 m height interval a maximum flight range (MFR) and a maximum flight duration (MFD) for an energy constrained (energy-model) and a water constrained bird (water-model). We examined to what extent the height distribution of echo densities could be predicted by the MFR and/or MFD for energy or water constrained birds. For statistical comparisons we calculated for each night a Spearman rank correlation (r_s) between echo density and the predicted values. We performed a general linear model analysis (GLM) with echo density as the dependent variable (log- and Z-transformed, s. below). The predicted variables (MFR, MFD) were Z-transformed in such a way that for each night the mean value was zero and standard deviation was 1. The height interval was introduced as a fixed factor and the Z-transformed MFR and MFD of the two models as covariates. Mean echo density per night was applied as a weight factor. SPSS 12.0 for Windows was used for statistical analyses.

Differences in the absolute values between the predicted maximum flight ranges according to energy and water consumption were not investigated. These values depend to a large extent on the various constants used in the model; e.g. using the formula for exhaled air temperature as published by Tielemann *et al.* (1999) for desert larks would considerably increase maximum flight range with respect to water loss.

Results

About 90% of all migrants recorded between the ground and 4000 m agl were flying above 1000 m, and more than 50% above 2500 m (Fig. 1). Favourable tailwinds occurred frequently above 2000 m agl, getting rare closer to the ground. Temperature ranged from 20 to 32°C on the ground and decreased gradually towards 2 to 5°C at 4000 m agl. Up to 2500 m relative humidity varied within a narrow range of 10 to 20%. Above 2500m variation in relative humidity increased to values between 5 and 50%. Air pressure decreased steadily with altitude and showed little variation from night to night (Fig. 1).

For both models, taking energy and water, respectively, as limiting factors, predictions of maximum flight range (MFR) were significantly correlated with the distribution of echo densities ($P<0.05$) in more than 50% of the nights (Fig. 2). The correlation coefficients themselves were highly correlated between the two models ($r_s=0.81$, $P<0.01$). Correlations with the maximum flight duration (MFD) were generally lower for the energy-model and clearly inferior for the water-model (Fig. 2). MFD between the models was much less but still significantly correlated ($r_s=0.14$, $P<0.01$). Later in the season the correlation coefficients between echo density and MFR’s for both models increased markedly (Fig. 3).

For the GLM-analysis we used the height interval as a fixed factor, MFR and MFD of the two models as covariates. The best model explained 43% of the variance including the height interval, the MFR from the energy-model and the MFD from the water-model (Table 1). The MFR from the energy-model explained 10 times more of the variance than the other two variables. In addition, we analysed the first 25 and the last 25 nights separately (6 March – 12 April and 13 April – 14 May 2003). For the first part of the season the GLM-analysis ended up with the fixed factor height interval and the covariate MFR from the energy-model as the best explaining factors (r^2_{adj}=0.19). For the second part of season the GLM-analysis resulted in the same variables as in the overall model (s. above), but the explained variance was considerably higher (r^2_{adj}=0.66).

Discussion

The MFR-predictions fitted the observed height distribution better than the MFD-predictions. This is not surprising, as the aim of a migratory bird should be to fly at levels were they can cover as much distance as possible, and not where they can stay in the air as long as possible. The MFR’s based on energy expenditure were very closely related to the tailwind support (r^2=0.98), but also MFR’s constrained by water consumption showed a strong correlation with the tailwind (r^2=0.83). The magnitude of correlation as well as the similarity between the models, is very close to the results found for nocturnal migration over southern Israel (Liechti *et al.* 2000). In the Israel data there was a tendency for the water-model to be slightly superior to the energy-model. Although in Mauritania temperatures were higher, particularly at low altitudes, and relative humidity was generally lower than in Israel, there was less evidence that migrants were choosing altitudes to save water (but see GLM-approach below).

As in both models wind was a major factor, we were interested to see, if the remaining variance could be related to other parameters. Therefore, we performed a GLM-approach, even though there might be some statistical objections. However, we considered measurements between height intervals and nights as independent. With the Z-transformation we eliminated the absolute difference between nights and reduced the problem of the zero values in the echo densities. The result confirmed the importance of the wind (energy-model). The additional effect of flying at levels with minimum water loss was highly significant, but with a low contribution to the total variance explained. If air temperatures are high (>22°) birds have to actively increase evaporative water loss to lose excess heat (Kvist *et al.* 1998). However, above the Sahara spring migrants fly at high altitudes, where wind conditions are mainly favourable and temperatures were relatively low (<20°); thus, heat stress was not very pronounced. A significant proportion of the remaining variance was related to height. This indicates that there are still height related aspects which are not yet considered in our model predictions (energy and water). This can be caused by the restricted power of a linear model, or other factors not taken into account in the model. Cost of ascending may cause birds to favour low altitudes with moderately good but not optimal conditions. For large birds climbing is more costly than for small birds. Therefore, the wind profit has to be larger for large birds to pay for their higher costs of climb. For some birds reduced oxygen pressure might become a relevant factor. In contrast to the former analysis by Liechti *et al.* (2000) the GLM-approach allowed us to show that there was an additional effect of water constraint in addition to the wind effect. This is in line with Carmi's *et al.* (1992) presumption that water constraint contributes to the selection of flight altitudes by nocturnal migrants above the desert. The significant increase of the suitability of our model predictions with the season is not easy to understand. The increasing temperatures could be responsible for the increasing effect of the water constraint, but why do predictions based on the energy budget alone also perform much better? Wind conditions did not show any obvious seasonal trend. We might argue that later in the season the real long distance migrants breeding at high latitudes pass through, and they might be better adapted to optimal flight strategies than those breeding in the Mediterranean region. However, this would mean that early migrants waste energy, and therefore also time, which is at least doubtful. Perhaps a differential analysis of radar echoes (water bird type versus song bird type) might throw some light on this question.

We have not considered Klaassen & Biebach's (2000) results on the same subject using more or less the same model settings. This analysis was based on recordings of bird migration at five different sites for a few days in the Egyptian desert using a small ship radar adapted with a parabolic antenna to perform vertical fixed beam measurements (Biebach et al. 2000). Distances of the targets crossing the beam were collected manually. As the radar recordings did not account for the variation of detection probability with distance and did not incorporate the surveyed volume with respect to target size, these quantitative estimates must be considered with great reservation. Without any information on echo signature, direction and speed of the targets it was not possible to distinguish between birds and insects (cf. Bruderer 1995a). The estimate of migration densities in this radar study resulted in figures which are 10 - 40x higher than those of moon-watch observations by Biebach et al. 1991) at the same site and at various other sites (Kiepenheuer, 1965) in the eastern Sahara. Biebach et al. (2000) estimates are also much higher than our density measurements of nocturnal migration in Israel (which certainly comprise the highest densities to be expected in the Palaearctic-African bird migration system; Bruderer & Liechti 1995). Simultaneous comparison between moon-watching and radar observations revealed factors differing by 1 to 3 depending on the height distribution of the birds (Liechti et al. 1995). As the migration intensity in the Biebach et al. (2000) study was (expectedly) very high at low altitudes, where moon-watching is very reliable, there is a strong suspicion that their radar picture was heavily contaminated with insects. Simply neglecting the different detection probabilities of different targets and not identifying the echoes at least at the insect/bird level will produce data, which are very difficult, if not impossible, to evaluate. We therefore refrained from discussing their results.

Our results confirm that wind is the most important factor for determining flight altitudes in bird migration. Many authors have used wind conditions averaged over time or space to calculate potential flight ranges (e.g., Stoddard *et al.* 1983, Moore & Kerlinger 1987, Piersma & Van de Sant 1992). However, migratory birds are able to select specific heights with favourable tailwinds within actual flight (Bruderer *et al.* 1995b). This implies that up to now most flight range calculations, if not all, have been too conservative. There is still a gap between what we expect from optimality theory and what a bird is able to perform in the field. Therefore, we should incorporate models based on individual reaction norms (e.g. Bruderer *et al.* 1995b) with optimal model predictions.

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Table 1. Univariate general linear model analysis of measured echo densities in relation to model predictions. Echo densities were log- and Z-transformed (Z-lnDen). Variables were Z-transformed to correct for different variances between nights (s. method). Z-MFRE = Z-transformed maximum flight range for the energy-model, Z-MFDW = Z-transformed maximum flight range for the water-model, H200 = height interval introduced as a fixed factor. $r^2_{adj.} = 0.429$; weighted by least squares regression - weighted by MD (=mean echo density per night).

Dependent Variable: Z-lnDen

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1611.9(a)	21	76.8	36.8	.000
Intercept	.0	1	.0	.0	1.000
Z-MFRE	402.3	1	402.3	192.7	.000
Z-MFDW	40.5	1	40.5	19.4	.000
H200	401.3	19	21.1	10.1	.000
Error	2041.9	978	2.1		
Total	3653.8	1000			
Corrected Total	3653.8	999			

Figure 1. Height profiles of the echo density, tailwind component, air temperature, relative humidity and air pressure measured at the oasis of Ouadâne, Mauritania. Mean and standard deviation over the study period (6 March to 15 May 2003) are given for each height interval of 200 m for the echo density. The 10% and 50% height level is given by arrows, indicating the proportion of birds flying below this level. Median, quartiles and 90% ranges per 200m intervals are given for the other variables (n=50).

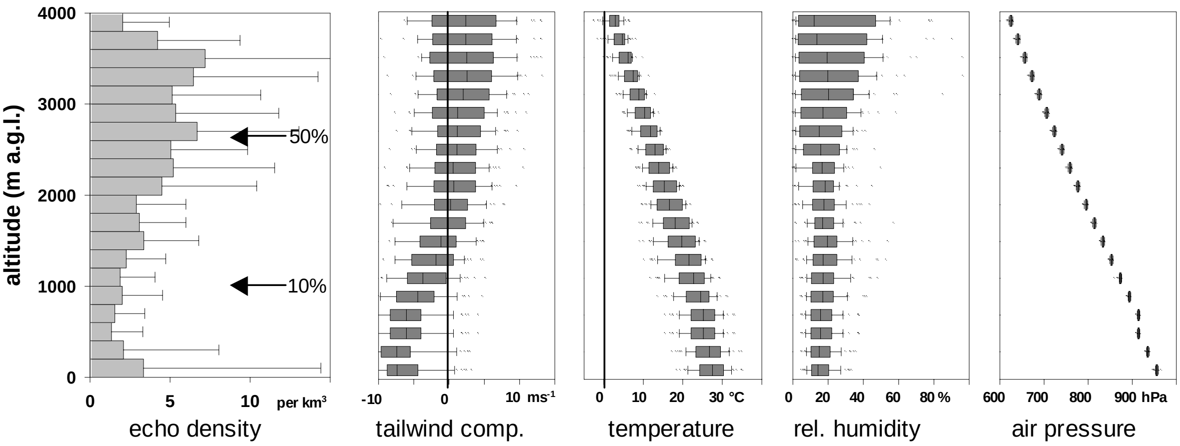


Figure 2. Distribution of the correlation coefficients calculated for each night (n=50) between the height distribution of the echo densities (n=20) and the predicted maximum flight ranges (MFR) and maximum flight durations (MFD) based on the energy and water-model (s. method). Median (line), quartiles (box), 90% ranges (whiskers) and outliers (dots) are given. The dashed line indicates the 5% significance level.

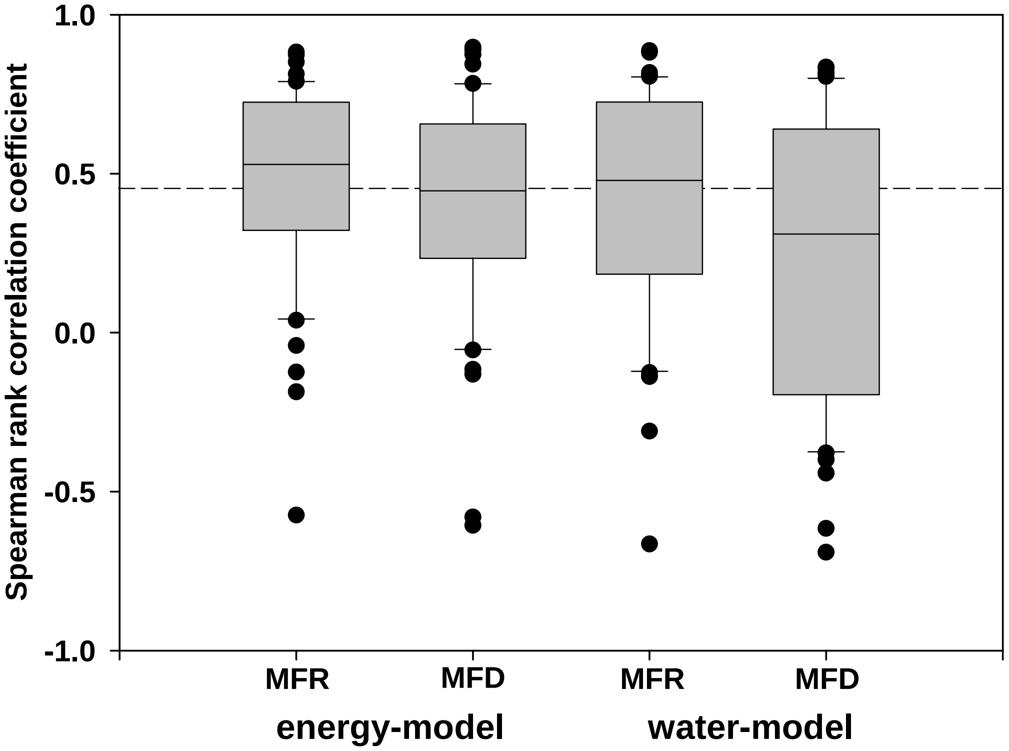
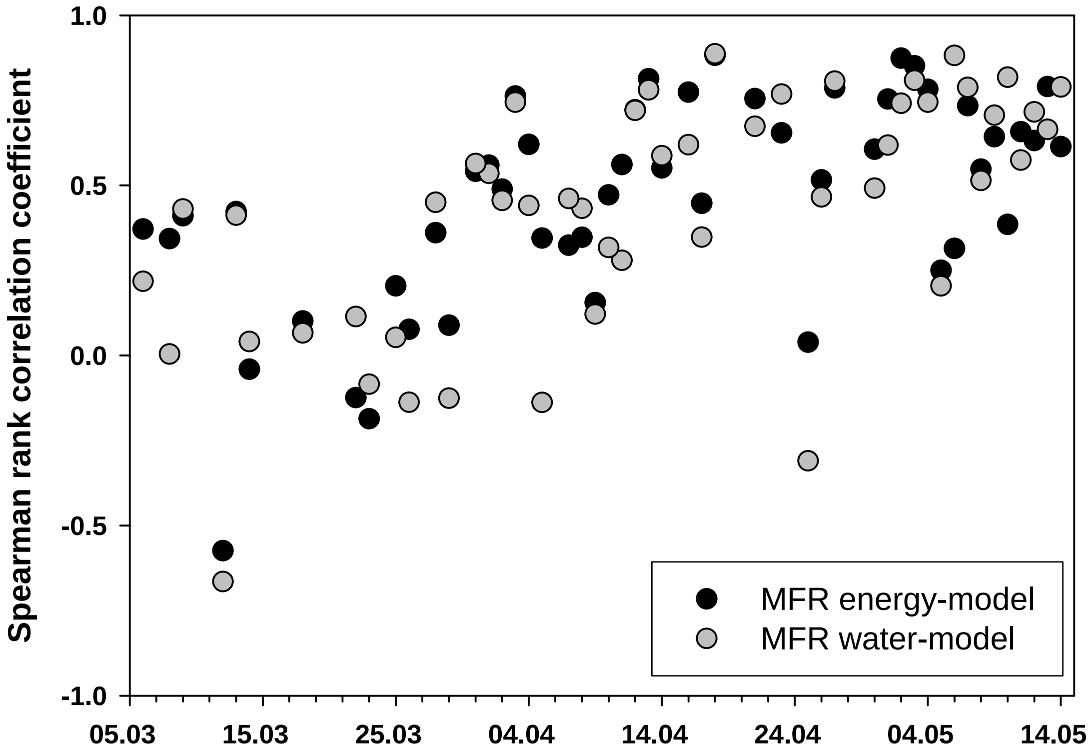


Figure 3. Correlation coefficients in the course of the season calculated for each night (n=50) between the height distribution of the echo densities and the predicted maximum flight ranges (MFR) based on the energy and water-model (s. method).



VI

Wind governs flight altitude of trans-Saharan migrants – no evidence for a water saving strategy

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Flapping flight is the most expensive activity for a bird in respect of energy and under certain conditions also of water consumption. During flight, atmospheric conditions strongly influence the energy and water budget. By adjusting their flights spatially and temporally with respect to these conditions, birds can reduce their energy and water consumption considerably. There is ample evidence that birds select their flight altitudes according to favourable winds, but it has been questioned, whether on long-distance flights water stress has an effect on their migration strategy. We quantified with radar the spatial and temporal pattern of songbird migration across the western Sahara at an oasis and at two bare desert sites in autumn and spring. Based on a physiological flight model, we predicted optimal flight altitudes with respect to water and energy consumptions. Migrants crossing the Sahara in autumn face the trade-off between (a) favourable winds coupled with hot and dry air at low altitudes and (b) humid and cold air combined with unfavourable winds higher up. In spring, favourable winds coincide with the cold and humid air at high altitudes. In autumn nearly 90% of the nocturnal songbird migration occurred at altitudes below 1000 m above ground level, indicating a clear preference for energy saving, while ignoring a possible water stress. The model aiming for minimal water consumption predicted a mean flight altitude of 3400 m under the given meteorological autumn conditions in the Sahara. In spring, songbirds flew considerably higher than in autumn, in accordance with both model predictions considering energy and/or water as the limiting factor. However, their preference for tailwind in autumn, despite the hot and dry air, emphasizes the importance of energy savings and invalidates the hypothesis that water stress might be an important factor. Nevertheless, we suggest that during daytime a combination of high-energy requirements due to air turbulences and possibly increased water demands due to warm and dry air prevent songbirds from prolonging their nocturnal flights regularly into the day, in spite of harsh resting conditions on the ground.

Keywords: passerine migration; Sahara; energy and water costs; flight altitude; radar

Introduction

Flapping flight is the most expensive activity for a bird with respect to energy consumption (Butler 1991) and under certain conditions also for water expenditure (Engel 2005). For migratory birds, at least the long distance migrants, the economic use of these resources during flight might be crucial for survival. The consumption rates per kilometre flown are substantially influenced by meteorological conditions en route. Energy expenditure is affected mainly by wind, air turbulences and air density

(Pennycuick 1989; Kerlinger & Moore 1989; Bruderer *et al.* 1995; Liechti & Bruderer 1998; Liechti *et al.* 2000; Green 2003; Hedenström *et al.* 2005; Liechti 2006), whereas water loss depends on air temperature, oxygen concentration and relative humidity (Kerlinger & Moore 1989; Carmi *et al.* 1992; Klaassen 1995; Carmi & Pinshow 1995; Klaassen 1996; Klaassen *et al.* 1999; Klaassen 2004). As these meteorological factors vary in time and space, migratory birds are expected to be selective for time periods and flight altitudes to minimize energy costs or water loss or, if possible, both.

Energetic flight costs and the environmental factors affecting the energy consumption are in general well understood (Masman & Klaassen 1987; Pennycuick 1989; Rayner 1990; Hedenström & Alerstam 1995; Klaassen 1996; Weber & Houston 1997; Pennycuick 1998; Thomas & Hedenström 1998; Klaassen *et al.* 2000; Rayner 2001; Kvist *et al.* 2001; Wikelski *et al.* 2003; McWilliams *et al.* 2004; Hedenström *et al.* 2005); on the contrary the water budget of migrating birds is poorly understood (Michaeli & Pinshow 2001), though intensive wind tunnel experiments have been performed, e.g. Biesel & Nachtigall (1987), Rothe *et al.* (1987), Kvist (2001) and Engel (2005).

Klaassen *et al.* (1999) introduced a physiological model based mainly on the water expenditure model by Carmi *et al.* (1993) and the flight power model from Pennycuick (1989). Flight range predictions were calculated either according to energy consumption alone (E-model) or according to a combination of water and energy consumption (WE-model). Several studies applied the model to field data, investigating the trade-off between energy and water consumption by comparing altitude distributions of migratory birds with theoretically optimal flight altitudes predicted for energy and/or water constraints (Liechti *et al.* 2000; Klaassen & Biebach 2000; Liechti & Schmaljohann in press). They found fairly good correspondence between model predictions and real flight altitudes, but all three studies revealed similar results for both model predictions (E- and WE-model). In all these studies favourable wind as the main energetic factor occurred always at altitudes with little water stress (Klaassen 2004), hence it could not be properly distinguished whether energy or water was the limiting factor.

We investigated western Palaearctic songbirds migrating across the western Sahara. Birds wintering south of the Sahara encounter two severe ecological barriers on this flyway, i.e. the Mediterranean Sea and Sahara desert (Moreau 1961; Moreau 1972; Bairlein 1988; Biebach 1990; Spina *et al.* 1993). Before crossing, birds replenish their fat and protein reserves to overcome the lack of refuelling sites during the future barrier crossing (Ward 1963; Odum 1963; Fry *et al.* 1970; Bairlein 1988; Piersma 1990; Jenni & Jenni-Eiermann 1998). We quantified bird migration across the western Sahara in space and time by radar (Schmaljohann *et al.* 2006), and determined altitudinal profiles of the weather variables. The quite stable wind regime in spring and autumn reveals an almost experimental situation. In autumn, birds encounter favourable but warm and dry winds at low altitudes (trade wind zone) and unfavourable but cold and relative humid winds at high altitudes (anti-trade wind). The E-model would predict largest flight ranges where favourable winds occur, i.e. at low altitudes, whereas the WE-model would advise migrants to fly at high altitudes to minimize water loss. Thus, the two models will give contradictory predictions for autumn. In spring migrants are expected to fly high in the anti-trade wind in cool and humid air, hence, both models would predict similar flight altitudes.

The large majority of trans-Sahara migrants are songbirds crossing the desert mostly during the night (Schmaljohann *et al.* 2006), whether this migratory pattern is shaped by high diurnal flight costs is unknown. Although diurnal migration of songbirds (except hirundines) is a rare event in the western Sahara, some prolong their migratory flights on days with favourable winds (Schmaljohann *et al.* in press). Contrary to autumn when only few songbirds migrated in daytime, up to 17% of the whole songbird migration occurred during the day in spring (Schmaljohann *et al.* 2006).

In this study we will focus on two questions: (1) Do songbirds select altitudes to minimize their energy or their water budget? (2) Do songbirds avoid diurnal flights in the desert to save energy or water (or both)? We applied the physiological model introduced by Klaassen *et al.* (1999) under the specific atmospheric conditions encountered in the western Sahara. We also included a simple wind profit model (Wind-model) calculated within Klaassen *et al.* (1999) model following Piersma *et al.* (1990). We calculated theoretical altitudinal bird distributions for day- and nighttime following the E-, WE- and Wind-model, and compared these different theoretical distributions with measured altitudinal distributions of songbirds.

Materials and methods

Study area and periods

Data were collected in Mauritania close to the oasis Ouadâne (oasis hereafter), located about 500 km east of the Atlantic coast (20°56' N, 11°35' W) and at two sites (Mohammed Lemna: 18°35' N, 08°38' W and Bîr Amrâne: 22°47' N, 08°43' W) 300 km further east in the plain sand desert. We refer to both sites as "desert sites" hereafter. The oasis is situated at a transition of sandy to rocky desert about 420 m above sea level (asl), there bird migration was measured in autumn 2003 (24.08. - 25.10.2003) and spring 2004 (15.03. - 10.05.2004). The observation periods at Mohammed Lemna (340 m asl) and Bîr Amrâne (270 m asl) were 19.09. - 30.09.2003 and 03.04. - 15.04.2004, respectively.

Quantification of songbird migration

We used the tracking radar "Superfledermaus" in a surveillance mode to record the spatial and temporal distribution of birds. Bird migration was quantified using the fixed beam method (Schmaljohann *et al.* submitted). At the oasis fixed beam measurements were carried out at a low and high elevation angle (11° and 79°) to every hour and at the two desert sites at three different elevation angles (8°, 28° and 79°) three times per hour. In doing so, high and low altitudes were surveyed with nearly the same effort. The resulting number of fixed beam measurements for autumn was 2680 at the oasis and 2064 at the desert site, for spring 2050 and 3971, respectively. The beam was directed towards West (270°), and thus perpendicular to the main migration direction (Schmaljohann *et al.* in press and see below). The recording time per measurement was 4 min and detection range for songbirds was restricted to 7 km (Schmaljohann *et al.* submitted). This fixed beam system allowed to collect the echo signature of each target crossing the beam and enabled us to distinguish between birds and insects on the basis of their echo signatures. This identification was essential as insect echoes made up a substantial proportion of all echoes. To quantify songbird passage, we selected only songbirds out of the detected birds according to their echo signature (= wing beat pattern) (Bruderer 1969; Bloch *et al.* 1981). Swallows and corvids differ in migration strategy (being mainly diurnal migrants) and flight type (resulting in distinctive wing beat patterns) from the majority of songbirds, i.e. Motacillidae, Turdidae, Sylvidae and others, and were excluded from the samples accordingly. For further information about quantifying bird migration see Schmaljohann *et al.* (submitted).

For the nighttime analyses we averaged songbird densities from 10 pm to 2 am per night (nighttime hereafter) and for daytime from 10 am to 2 pm per day (daytime hereafter) for each study site. Depending on the analysis (see below) densities of songbird migration were calculated for four or nine altitudinal intervals, respectively. We determined the flight directions of migrants by tracking single songbirds during night and day (Bruderer 1994; Liechti & Bruderer 1995). In autumn songbirds migrating during nighttime had a mean flight direction of 195° ± 3.3° (sd, n = 1402, mean vector length = 0.82) and during daytime (> 9 am and < 3 pm) of 212° ± 3.3° (sd, n = 242, mean vector length = 0.82), respectively. The differences between these two flight directions are insignificant in respect to the model predictions, and we simplified the mean flight direction for the whole autumn season of the corresponding two time periods as the overall mean of 198° ± 3.3° (sd, n = 1644, mean vector length = 0.81). We did the same for spring resulting in a mean flight direction of 3° ± 3.0° (sd, n = 1619, mean vector length = 0.84) [flight directions during nighttime: 4° ± 3.0° sd, n = 1247, mean vector length = 0.84; during daytime 358° ± 3.0° sd, n = 372, mean vector length = 0.84].

Meteorological data

We had two sources of meteorological data: (1) own measurements and (2) model data from the National Oceanic & Atmospheric Administration (NOAA hereafter).

(1) Radio sonde balloons launched at the oasis around midnight every night provided altitudinal profiles of air pressure, air temperature, and relative humidity up to about 6000 m above ground level (agl). Simultaneously, wind measurements were carried out (Bruderer 1994). Processing of the meteorological and nighttime songbird density data resulted in altitudinal profiles with nine successive altitude intervals of 500 m up to an altitude of 5000 m asl.

(2) Such on site radio sonde data do not exist for the two desert sites and not for the oasis at midday. For these sites and time periods we downloaded meteorological data from the NOAA; NCEP/DOE AMIP-II Reanalysis (http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html). Data were available for midnight (0 am) and midday (12 am) at four different pressure levels (925 mbar, 850 mbar, 700 mbar, and 600 mbar) representing four altitude intervals (ground level – 1150 m, 1150 – 2400 m, 2400 – 4000 m, and 4000 – 5000 m). Our measured songbird densities were adjusted to these four altitude intervals accordingly. No air pressure data were available, because the NOAA altitude intervals are determined by pressure. However, air pressure levels measured by the radio sondes at Ouadâne were very constant within the same altitude intervals in autumn and spring. The 95% confidence interval for each 500 m altitude interval was below 1.5 mbar for the autumn (n = 62 nights) and spring (n = 54 nights) season by using each night's mean air pressure per 500 m altitude interval. We, therefore, applied the measured night air pressure from the oasis to the midday and desert site analyses. To verify whether the NOAA and radio sonde data produced similar results, we analysed nighttime migration at the oasis with both meteorological data sets.

The models

We used three different models, i.e. wind-, energy-, and water/energy-model, to predict the migration flight altitude of songbirds across the Sahara during night- and daytime. Bruderer *et al.* (1995b) demonstrated that the tailwind component is a good predictor for the flight altitude of migrants. Due to the constant trade wind system in western Africa (with strong winds from the Northeast at low and the Southwest at high altitudes) we used the wind effect (Wind-model) as a predictor for the flight altitude instead of the tailwind component. The wind effect can be regarded as the speed at which a bird is passively transported towards its goal (or away from it). This speed component (ΔV) is based on the migratory direction (md; 197° in autumn and 3° in spring, see above), wind direction (wd), wind speed (V_w, m/s) and bird’s airspeed (V_a, m/s):

$$\Delta V = V_w \bullet \cos\alpha + \sqrt{V_a^2 - (V_w \bullet \sin\alpha)\,{}_a^2} - V_a\ ,$$

$$\alpha = wd \pm 180^\circ - md$$

according to Piersma *et al.* (1990), Klaassen *et al.* (1999) and Erni *et al.* (2002).

The energy (Pennycuick 1989) and water budget adaptations of bird’s flight (Carmi *et al.* 1992; Klaassen 1995; Klaassen *et al.* 1999) are more complex models than the Wind-model. The E-model predicts flight ranges depending on the energy reserves, energy expenditure (Pennycuick 1989) and the wind effect (Piersma *et al.* 1990; Klaassen *et al.* 1999) and thus, flight range is limited only by the available energy and highly dependent on the wind effect (Klaassen & Biebach 2000). We assumed that the songbirds compensated completely for wind drift. The WE-model calculates the water budget by air pressure, ambient temperature, relative humidity and the energy budget as in the E-model. In the WE-model flight ranges are, therefore, restricted by water (dehydration) or when mass reaches lean body mass. For calculating the different flight range predictions we used the computer program from Klaassen *et al.* (1999).

Model parameters

The model predictions were performed for a small trans-Sahara songbird migrant (Willow Warbler *Phylloscopus trochilus*) using mostly the same parameters as Carmi *et al.* (1992), Liechti *et al.* (2000), Klaassen & Biebach (2000) and Landys *et al.* (2000). Liechti *et al.* (2000) and Klaassen & Biebach (2000) showed that the model predictions for small and large songbirds in respect of altitudinal predictions were very similar. Therefore, we used only the Willow Warbler as a model bird species for the analyses. Input data for the Willow Warbler were, body mass 10 g, wingspan 0.17 m, wing area 0.0069 m^2, fuel fraction of initial body mass 0.50 (assuming 71% water content of lean tissue). The maximum water-loss fraction of initial water content was arbitrarily set to a rather conservative value of 60%. For the drag coefficient we used 0.18 after new results from Hedenström & Rosén (2003). For the expired air temperature we used its dependency on the ambient temperature found in flying European Starlings (*Sturnus vulgaris*) by Engel (2005) rather than the equation according to Berger *et al.* (1971), because our model species was a songbirds and Engel (2005) measured the expired air temperature while birds were flying and not after the flight. Expired air temperature was not allowed to exceed the assumed body temperature of 40°C. Otherwise the default values given by Pennycuick (1989) were taken. Fuel reserves from the model bird consisted of 70% fat, 9% protein, and 21% water, resulting in an energy density of 29 kJ/g and metabolic water yield of 1.00 g per gram of fuel (Klaassen 1996; Jenni & Jenni-Eiermann 1998).

Statistics

For each site, night, day and altitude interval, we computed the flight range estimates according to the Wind-, E- and WE-model. Thus, we received three theoretical altitudinal distributions based on the predicted flight ranges per site, night and day.

These flight range altitude distributions were taken as a qualitative index for the expected altitudinal distribution of songbirds. Absolute flight ranges calculated by the model should be treated cautiously, because (1) migrants increase the relative proportion of energy derived from fat when fasting and this will change the power curve relating energy expenditure to flight speed and predictions derived from it (Jenni & Jenni-Eiermann 1998). (2) Flight costs increased at a lower rate with an increase in fuel load than indicated by the flight power model (McWilliams *et al.* 2004). E.g., Kvist *et al.* (2001) showed that heavy birds used less power than expected by flight range model calculations. This was suggested to be either due to a higher muscle efficiency to convert fuel to mechanical work increasing with fuel load (Kvist *et al.* 2001) or to a change in the wing lift coefficient or wingbeat frequency (Rayner 2001). Furthermore, important model variables have a paramount effect on the flight range and are additionally hard to estimate under natural conditions, i.e. expired air temperature, fuel energy density, and oxygen extraction coefficient (Klaassen *et al.* 1999). Klaassen & Biebach (2000) showed, that variation in some model parameters (i.e., exhaled air temperature, oxygen extraction and water reserve) influenced the absolute range prediction but not its relative distribution. To compare the outputs of the three different models (E-, WE- and Wind-model) and to minimise the shortcomings of the absolute flight range calculations, we made only relative comparisons.

We correlated the predictions of the Wind- and E-model per site for night- and daytime, to test whether the E-model was highly determined by the wind as in Klaassen & Biebach (2000). Since all R^2-values were above 0.95, and results were almost identical to the wind model, we present only the Wind-model in the result section for the sake of simplicity.

To characterize the qualitative index, we calculated a Spearman rank correlation between the model predictions and the measured songbird densities of the different (four or nine) altitudinal intervals. Only night- and daytime periods with ten or more songbirds registered by radar were considered; otherwise the sample for the altitudinal distribution of songbirds was not regarded as representative. To summarize the results of the Wind- and WE-model, we present the distribution of the Spearman rank correlations per season and time of day in box plots. Since only a few daytime periods contained more than nine songbirds, we do not present their Spearman rank correlations in boxplots. The Wilcoxon signed rank paired test was used to test for differences between the Wind- and the WE-model.

To test whether the weather conditions varied between night and day, we produced a time series analysis (autocorrelation) for the air temperature, relative humidity and wind-effect of the NOAA data for the corresponding four altitudes with values from midnight and midday. To explore whether songbirds have a higher water loss in autumn or spring we used the "net rate of water loss" output variable given by Klaassen *et al.* (1999) per nighttime from the altitude interval with the highest songbird density of the nights with more than nine recorded songbirds. Statistics were calculated using the statistical software package R (R Development Core Team 2006).

Results

Songbird migration

In autumn, nocturnal songbird migration was highly concentrated (90%) within the lowest 1000 m agl at the oasis, whereas in the plain desert (Mohammed Lemna) altitudinal distribution was scattered over a larger range and higher up (Fig. 1). This difference remained even when comparing the same time period (not shown). Spring nighttime migration took place at higher altitudes than in autumn and was less focused to one altitude interval, but was similar at the oasis and desert site (Fig. 1). In general songbird migration densities were much higher during the night than during the day (in autumn 96% flew at night near the oasis, 84% in the desert. In spring: oasis 83%, desert 81%). Songbird density was low during the day and the little migration that occurred, took place at higher altitudes than during the night in both seasons (Fig. 1). The required sample size of more than nine birds per day for analysing height distributions was achieved for daytime only once in spring at the oasis and three times at the desert site. In autumn the limit was not reached for daytime periods at all.

Meteorological profiles

In most nights air temperature within the lowest altitude interval (0.5-1 km asl) was well above 30° C in autumn (32 ± 4°; sd, n = 62), whereas in spring air temperature was on average 6°C lower than in autumn (26 ± 4°; sd, n = 54; Fig. 2). In autumn and spring relative humidity showed an increase with altitude combined with a high variation (Fig. 2). In autumn favourable winds for southward migration prevail at low altitude and deteriorated with increasing height (Fig. 3). In spring best winds for northward migration occurred around 1 – 2.5 km asl (Fig. 4).

Altitudinal distribution of model predictions

The flight range predictions based on the meteorological data from the radio sonde and NOAA correlated high significantly with p-values below 0.001 for the Wind- and WE-model. Correlation coefficients were high for autumn (R^2 = 0.4 for the Wind-model and R^2 = 0.54 for the WE-model), but low in spring (R^2 = 0.08 for the Wind-model and R^2 = 0.05 for the WE-model; sample size for autumn correlations were 232 and for spring 204, respectively). The quality to predict songbird's flight altitude was very similar over season (Fig. 3, 4 and 5). For the sake of simplicity, we do not distinguish between results derived from the radio sonde or NOAA meteorological data. Weather conditions during the night and day were very similar. All autocorrelations (lag 1) for the temperature, relative humidity and wind-effect were significant (<0.05) and had high correlation coefficients (lowest was 0.416, mean was 0.72 ± 0.14 (sd, n = 24)). Consequently, model predictions of nighttime and of subsequent daytime correlated highly (Tab. 1) and seasonal means for night- and daytime were very similar (therefore not shown).

In autumn the Wind-model predicted low-level migration, whereas according to the WE-model songbirds should select high altitudes for night- and daytime migration at the oasis and desert sites (Fig. 3). Thus, there was a conflicting prediction between the Wind- and the WE-model.

In spring both models forecasted migration at average altitudes (1 – 2.5 km) with best conditions for flying in respect of energy and water constraints for night- and daytime at both sites. Nighttime predictions of the two models did not differ in general (Fig. 4 and 5) and were very similar to daytime predictions (not shown).

Comparison of the model predictions

For autumn nighttime migration the Wind-model predicted the songbird altitudinal distribution significantly and clearly better than the WE-model, irrespectively of site (Fig. 5). The quality of the Wind-model had a median Spearman rank correlation >0.5 in autumn, whereas most Spearman rank correlations of the WE-model had a negative value. Negative correlation coefficients indicate, that the model predicted the reverse of the songbird altitudinal distribution (Fig. 5).

For spring nighttime migration both models showed a similar distribution of the Spearman rank correlations (Fig. 5). The theoretical net rate of water loss – calculated with Klaassen's *et al.* (1999) program – for nighttime migration was significantly higher in autumn than in spring (55 ± 13 mg/h; sd, n_{autumn} = 38; 28 ± 9 mg/h; sd, n_{spring} = 19; Wilcoxon singed rank test: W = 680, p-value < 0.0001).

Since daytime migration was weak at all sites and during both seasons, no statistical comparisons between the Wind- and WE-model were meaningful.

Discussion

(i) flight altitude of nocturnal migration

Meteorological conditions and for the first time altitudinal profiles of songbird densities were measured in the western Sahara. Since songbirds selected low flight levels with best wind support during the night and did not climb to high altitudes where water loss would be minimized, the hypothesis that water might govern flight altitudes of nocturnal autumn migrants crossing the Sahara is clearly rejected. In spring predictions of both models were similar, matching equally well songbirds altitudinal distribution.

In autumn, highest wind effect was found at low altitude combined with very high temperatures and low relative humidity, whereas conditions higher up deteriorated in respect of the energy expenditure but improved steadily in respect of water constraints. Predictions of the Wind- and WE-model were contrary (Fig. 2 and 3). Songbirds migrated to a high degree (90%) within the lowest 1 km agl (Fig. 1) as precisely predicted by the Wind- and not by the WE-model (Fig. 5). Therefore, we could prove for the first time, that the influence of the wind is more important than possible constraints of the water budget when crossing the Sahara during nocturnal flights. This is in line with several studies and models demonstrating that birds aloft choose altitudes with favourable winds (Alerstam 1990; Gauthreaux, Jr. 1991; Richardson 1991; Bruderer *et al.* 1995; Butler *et al.* 1997; Erni *et al.* 2005; Battley & Piersma 2005) and departure from stopover sites occurs mostly when tailwinds are prevailing (Erni *et al.* 2002; Schaub *et al.* 2004; Erni *et al.* 2005), for a detailed review see Liechti (2006). By choosing the appropriate wind for migration a bird can easily double its flight range and preserve half of the energy/water required for a given flight bout (Liechti & Bruderer 1998).

In spite of this advantage, the vast majority of songbird had to cope with air temperatures well above 30°C and relative humidity of 30%. The extent of water stress depends on the relative humidity, ambient temperature and flight duration. In wind tunnel experiments pigeons and European Starlings (*Sturnus vulgaris*) became reluctant to fly at about 25°C (Hirth *et al.* 1987; Ward *et al.* 1999; Engel 2005). After Berger & Hart (1974) birds experiencing temperatures of 35°C might lose three- to four-times the amount of water via the lungs in flight than is produced metabolically by burning fat, see also Torre-Bueno (1978). Only at low temperatures of 10°C the net water loss was supposed to be negligible by Biesel & Nachtigall (1987). Klaassen *et al.* (2000) estimated that Thrush Nightingales (*Luscinia luscinia*) flying for 12 hours in a wind tunnel at temperatures between 16 and 23°C did not dehydrate, see also Kvist *et al.* (1998), whereas according to Biesel & Nachtigall (1987) pigeons remain flying only for 2 hours at 25°C due to dehydration. In outdoor experiments, pigeons flew freely for more than 2 hours at temperatures around of 27°C (Michaeli & Pinshow 2001), indicating that results of wind tunnel experiments cannot so easily be applied to free flying birds, probably because a wind tunnel-flight is more stressful than a free-flight (Ward *et al.* 1999; Liechti & Bruderer 2002; Engel 2005). Only little is known about flight duration of freely migrating songbirds, e.g. small thrushes (*Catharus* spp.) flew up to 8 hours per night (Cochran *et al.* 1967; Wikelski *et al.* 2003). For the autumn migrants flying in high temperatures, short flight steps (few hours) would not help to circumvent dehydration, because there is virtually no possibility to replenish water reserves at stopover sites in the desert.

According to WE-model birds flight range is about three-times shorter at the lowest altitude than at highest one. However, migration occurred at altitudes with best wind indicating clearly that songbirds selected flight altitude in respect of the energy and not water consumption. Assuming that the model assumptions are correct, we hypothesize that songbirds do usually not experience water stress situations when crossing the Sahara during their nocturnal migratory flights.

Klaassen & Biebach (2000) studied the altitudinal distribution of songbirds in Egypt also during autumn. In contrast to our findings their models predicted similar optimal flight altitudes for energy and water-energy restricted models. In Egypt the trade winds blowing at low altitude from the Northeast are enriched with humidity from the Mediterranean Sea and temperatures were lower than in our study. Migrants face favourable winds and high humidity at low altitudes during autumn migration. At higher altitudes the conditions for migration deteriorate in respect of the energy and water consumption, because the anti trade coming from the interior of the Sahara is dry and has a strong headwind component for autumn migrants. Therefore, migrants do not face the trade-off between advantageous flight conditions in respect of energy consumption at low altitude and favourable conditions in respect of water constraints at high altitudes, as they do in the western Sahara in autumn. In the western Sahara, the air mass has got a very low relative humidity, due to its large distance to the Mediterranean Sea (more than 2000 km). Unfortunately, the radar data on bird distributions used by Klaassen & Biebach (2000) and collected by Biebach *et al.* (2000) comprise some major methodological shortcomings (1. no echo identification at the bird-insect level, 2. unknown surveyed space [in distance and width], 3. neglecting different detection probabilities of different echo sizes; for further information see Bruderer (1997), Liechti & Schmaljohann (in press) and Schmaljohann *et al.* (submitted). We, therefore, disclaim discussing their results, particularly as Klaassen (2004) stated, that possible existence of water stress couldn't be confirmed or refuted by this work.

In spring at both sites the model predictions were similarly distributed, although the Wind-model was slightly, but not significantly, better than the WE-model (Fig. 5). Most songbirds migrated at medium altitudes (Fig. 1) and the mean seasonal altitudinal distribution corresponds well with the mean seasonal predictions of the two models (Fig. 1 and 4). The weak dominance of the Wind- against the WE-model is in accordance with similar studies about nocturnal spring migration (Liechti *et al.* 2000; Liechti & Schmaljohann in press).

(ii) costly daytime migration

Daytime migration of songbirds is considerably weaker than nighttime migration. We hypothesize that during the day the potentially high flight costs in respect of energy and water consumption restrict songbird migration to nighttimes.

Due to the low density of diurnal songbird migration, and thus small sample sizes, it was not advisable to analyse diurnal altitudinal distributions on a daily basis. The seasonal means of altitude distributions showed considerably higher flight levels during the day than at night (Fig. 1). As the Wind-model predictions did hardly differ between day- and nighttime (see results and Tab. 1), other factors than wind must have caused this shift towards higher flight levels. Conditions for migration deteriorate in the course of the day for songbirds, because air turbulences arise from the increasing solar radiation. Flying in these turbulences is more costly for small birds than flying in laminar air layers as they prevail at night (Kerlinger & Moore 1989). Furthermore, ambient air temperature increases and additionally the solar radiation might heat up the songbirds in the air, increasing the bird's water consumption. As both costs decrease with altitude, this might cause birds to fly high during the day.

Songbird daytime migration was more pronounced in spring than in autumn (though not so clearly at the desert site; Fig. 1), and the occasional diurnal flights in spring were strongly correlated with favourable winds at high altitudes (Schmaljohann *et al.* in press). In addition, the potential net water loss (Klaassen *et al.* 1999) during the day at the altitude with best wind effect reveals significantly higher values for autumn (44.1 ± 17.7 mg/h; sd, n = 61) than for spring (32.5 ± 11.7 mg/h; sd, n = 54; Wilcoxon signed rank test: W = 2422, $p < 0.0001$). This holds not only for the day, but also for the night when songbirds experienced a higher net water loss at altitude with best wind in autumn than in spring (s. results). We suggest that most songbirds do not prolong their migratory flights in autumn into the day, because the additional water costs of flying instead of resting (Engel 2005) would lead to a water stress situation for the songbirds, as suggested by Carmi *et al.* (1992). This idea is supported by some ground observations (Bairlein 1987; 1988; Bairlein & Totzke 1992) and model calculations (Carmi *et al.* 1992), for review see (Klaassen 2004). In comparison to autumn, spring migrants have the advantage of lower water stress during the nocturnal, as well as during potential diurnal flights. This may be the reason why spring songbird migrants can take the advantage of favourable wind conditions to prolong their flight into the day, while autumn migrants are mainly forced to save their water during the day by resting on the ground.

Several studies have claimed that water stress is a limiting factor for long nonstop migration under high temperatures, especially the Sahara crossing (Biesel & Nachtigall 1987; Biebach 1990; Bairlein & Totzke 1992; Carmi *et al.* 1992; Engel 2005). Since dehydration is difficult to detect directly in birds, the body water content is an insufficient indicator of water stress (Klaassen 2004 and references therein), special behavioural adaptations of migrants might indicate the risk of dehydration, e.g. drinking immediately upon arrival (Pennycuick *et al.* 1999) or escaping the blazing sun by migrating mainly nocturnally when crossing the desert (Klaassen 2004; Schmaljohann *et al.* 2006). At the oasis 65 out of 1409 mistnetted songbirds from both seasons had very little breast muscle but still reasonable fat reserves [fat class ≥3 and flight muscle class ≤1 according to Kaiser (1993) and Bairlein (1994)]. Since catabolizing protein yields a higher water output per unit energy than catabolizing fat (Klaassen 1996; Jenni & Jenni-Eiermann 1998), this may indicate that songbirds did catabolize protein for water production when crossing the Sahara, as suggested by Klaassen (2004).

Songbirds clearly preferred to minimize energy costs for migration despite the hot and dry air, which invalidates the hypothesis that water stress might be an important factor for the altitude choice when crossing the Sahara. We suggest that a combination of high energy (air turbulences) and high water (warm and dry air, solar radiation) costs might prevent songbirds from prolonging their nocturnal flights regularly into the day. In spite of harsh resting conditions on the ground, one may wonder, that it pays off to spend the daytime on the ground, instead of continuing the migratory flight.

More experimental work is needed (e.g. in wind tunnels) to answer the questions how birds (a) cope with the extreme atmospheric conditions on the ground during the day and (b) which factors are responsible for the preference of nighttime migration.

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Table 1. Correlation summary of model prediction from nighttime and subsequent daytime.

		Wind-model	Water-Energy-model
autumn	oasis	$R^2 = 0.70$, $p < 0.0001$, $n = 310$	$R^2 = 0.80$, $p < 0.0001$, $n = 310$
	desert	$R^2 = 0.70$, $p < 0.0001$, $n = 50$	$R^2 = 0.85$, $p < 0.0001$, $n = 50$
spring	oasis	$R^2 = 0.47$, $p < 0.0001$, $n = 280$	$R^2 = 0.37$, $p < 0.0001$, $n = 280$
	desert	$R^2 = 0.56$, $p < 0.0001$, $n = 105$	$R^2 = 0.51$, $p < 0.0001$, $n = 105$

Figure 1. Altitudinal distribution of songbird migration densities as seasonal means with standard errors (black and white lines) for night- (left side) and daytime (right side). X-axes for night- and daytime migration differ in unit of density for sake of clearness.

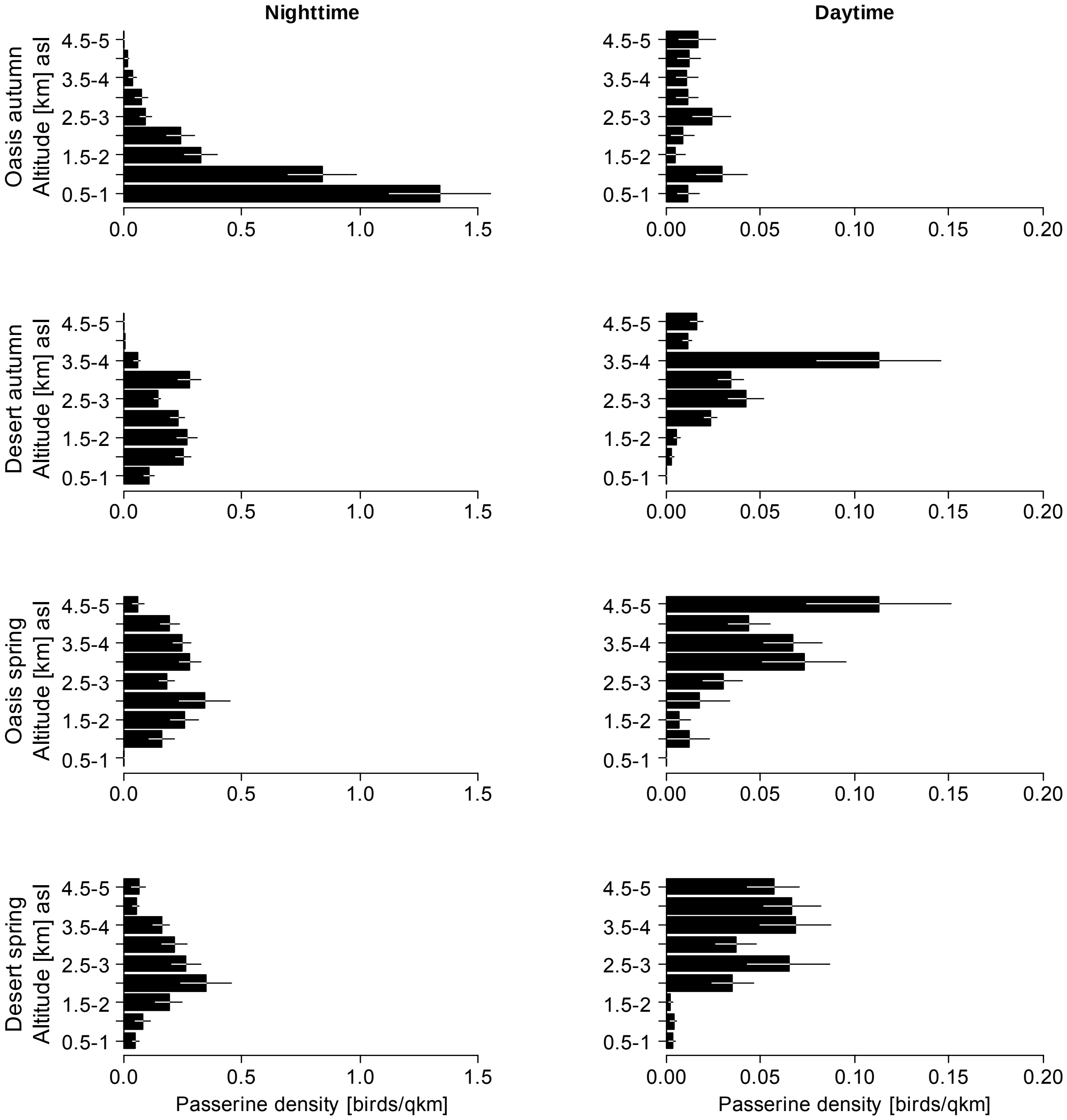


Figure 2. Altitudinal profiles of air temperature, relative humidity and air pressure at the oasis in autumn (upper, 62 nights) and spring (lower, 55 nights). Data are from own radio sonde.

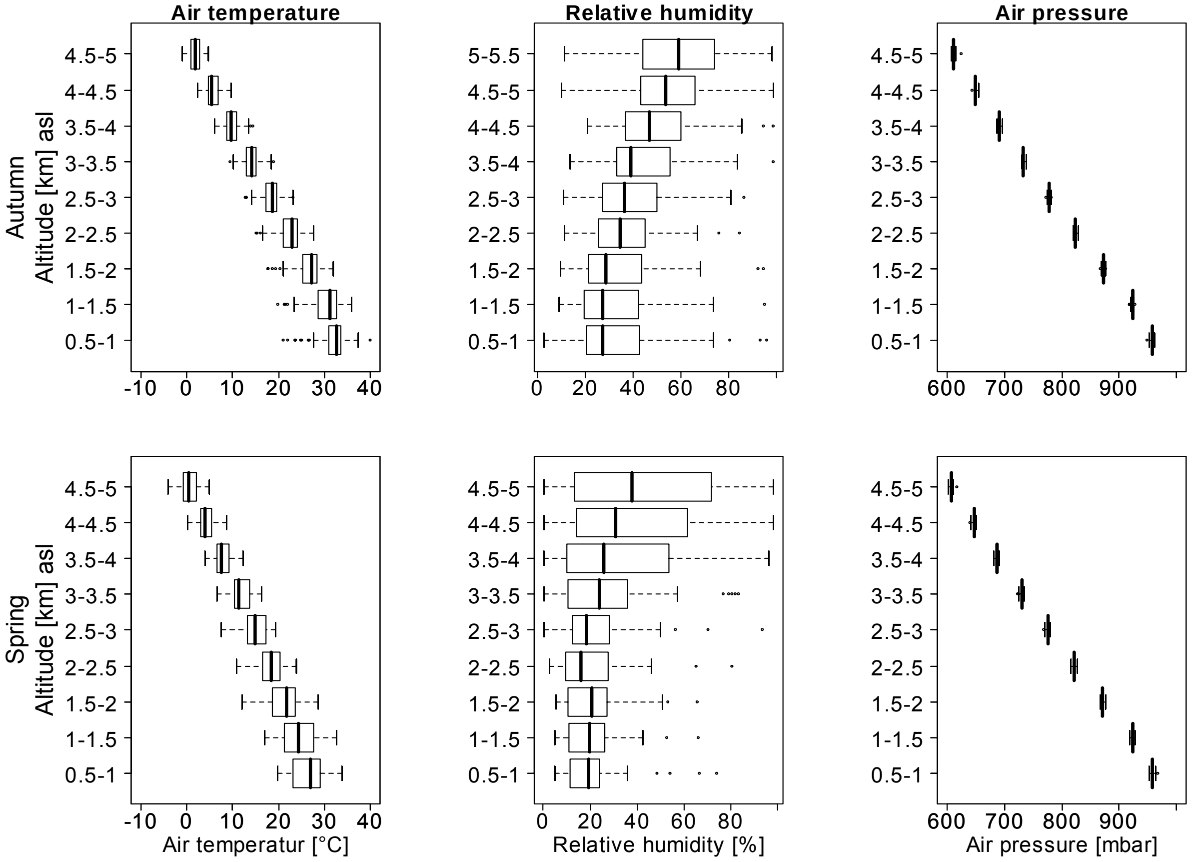


Figure 3. Altitudinal distribution of flight range predictions as seasonal means with standard errors (black and white lines) for nights in autumn (62 nights) at the oasis of energy-model (E-model), water/energy-model (WE-model) and wind effect-model (Wind-model) for the radio sonde (upper) and NOAA data (lower). Model predictions were very similar for daytime (not shown).

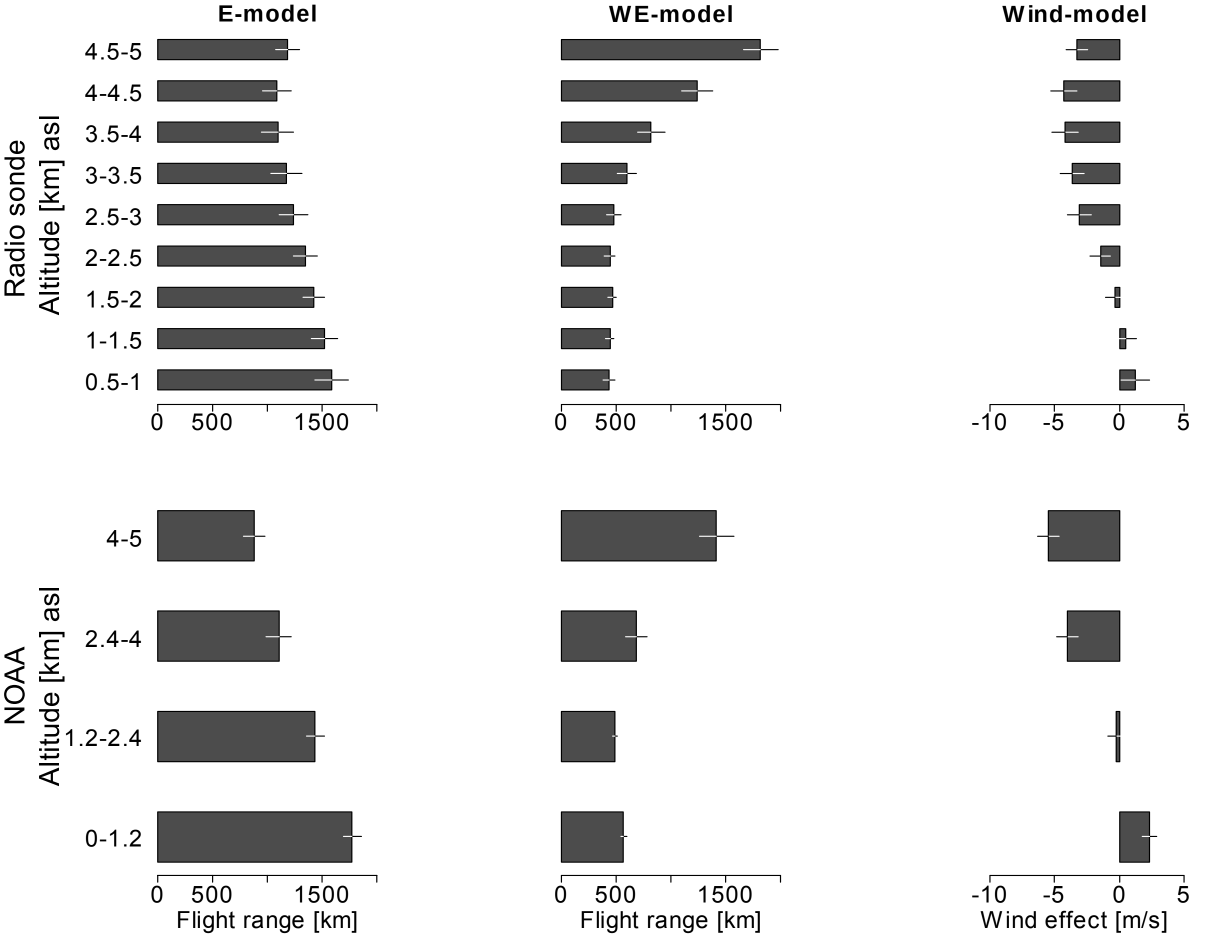


Figure 4. Altitudinal distribution of flight range predictions as seasonal means with standard errors (black and white lines) for nights in spring (54 nights, on 26.03.2004 no radar measurements were carried out) at the oasis of the energy-model (E-model), water/energy-model (WE-model) and wind effect-model (Wind-model) for the radio sonde (upper) and NOAA data (lower). Model predictions were very similar for daytime (not shown).

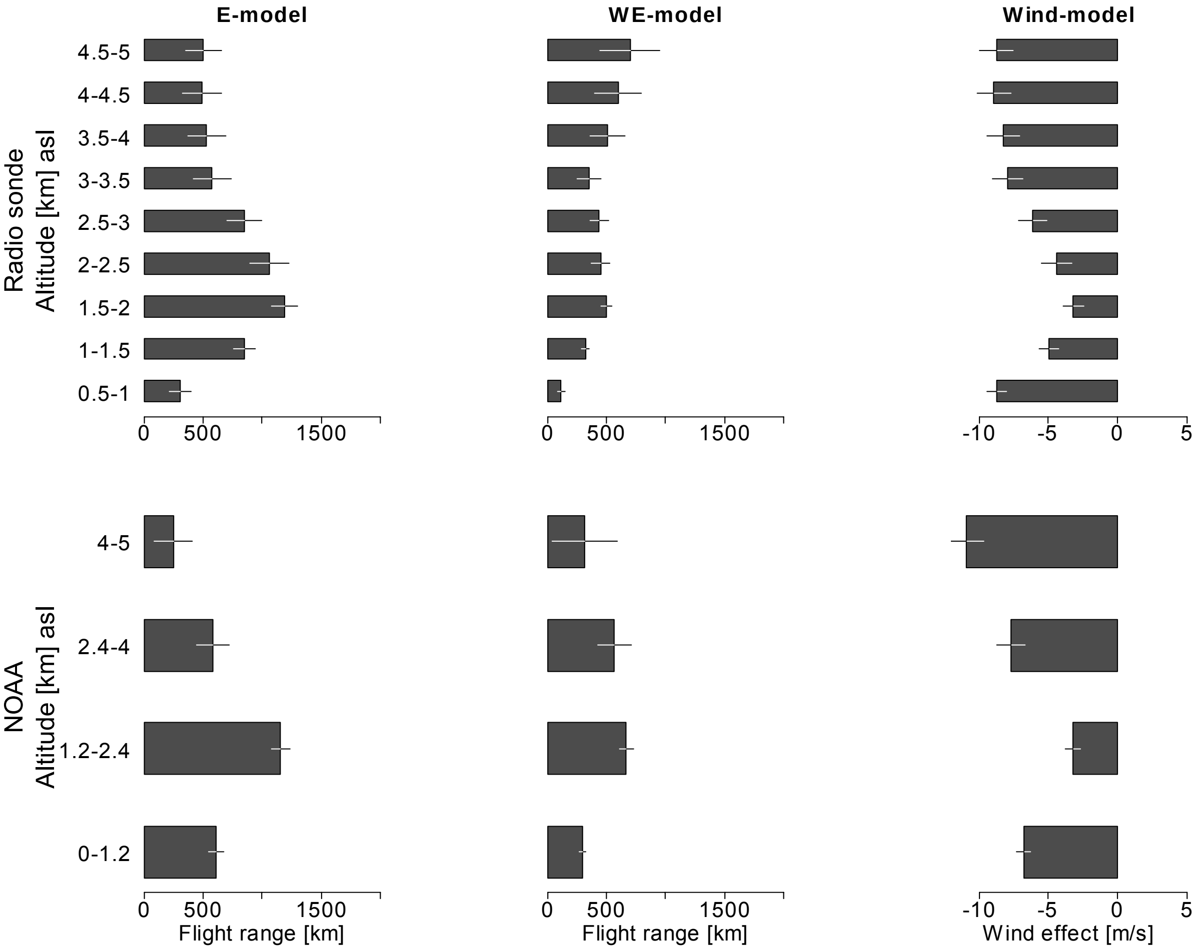
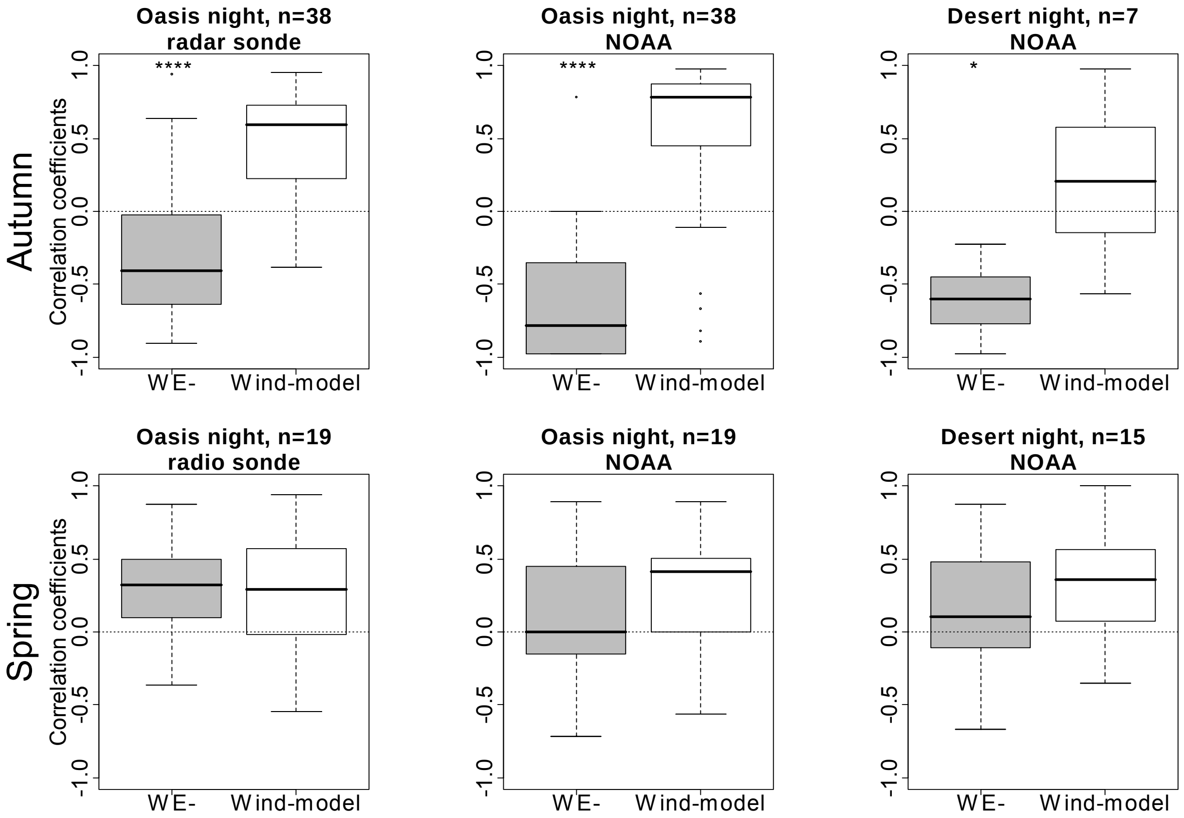


Figure 5. Distribution of correlation coefficients between the altitudinal profiles of model predictions of the water/energy-model (WE-model) and wind-model (Wind-model) for autumn (upper) and spring (lower) for all sites. Boxplots on the left side refer to radio sonde and boxplots in the middle and on the right to NOAA data, respectively. Dashed line indicates zero. Significant differences are indicated by * p < 0.05 and **** p < 0.0001.



VII

First records of Lesser Black-backed Gulls (*Larus fuscus*) crossing the Sahara non-stop

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Lesser Black-backed Gulls (*Larus fuscus*) migrate regularly along coastlines or the Nile to their wintering grounds in sub-Saharan Africa. They usually avoid the interior of the Sahara, but occur occasionally far inland when moving upstream along rivers. We discovered several flocks of Lesser Black-backed Gulls crossing the western Sahara about 500 km east of the Atlantic coast. Their concentrated flight directions along a northeast-southwest axis indicate that the gulls were on an intended migratory flight and not incidentally drifted inland. Flocks profited from tailwinds and some of them gained high flight speeds of up to 90 km/h. Warmest temperature encountered when crossing the study site was 13°C due to relative high flight altitudes (mean: 3500 ± 730 m, n = 8). Thus, Lesser Black-backed Gulls migrated under favourable conditions in respect of the energy and water consumption. Our observations strongly suggest that the gulls performed long non-stop flights between the eastern Atlantic coast and the Mediterranean Sea.

Keywords: Lesser Black-backed Gull; Sahara; non-stop migration; radar

Introduction

The Lesser Black-backed Gull is the only large gull from the western Palaearctic wintering regularly in sub-Saharan Africa (Malling Olsen & Larsson 2004). The eastern subspecies, *Larus fuscus fuscus*, breeding mostly at the Baltic Sea, flies around the Sahara along the eastern flyway following the Nile and the Red Sea to reach its wintering sites in eastern Africa (Urban et al. 1986; Moreau 1967; Malling Olsen & Larsson 2004). The western subspecies, *L. f. intermedius* and *graellsii*, occur at nearly all shorelines of Western Europe. Their major winter range is the Atlantic coast from France to Mauritania, but many prolong their migration to the coasts of Nigeria and the Gulf of Guinea (Malling Olsen & Larsson 2004). These African winter quarters suggest that Lesser Black-backed Gulls avoid the harsh conditions in the interior of the desert on their flights to the wintering grounds. There are, however, some scarce observations of both subspecies in the interior of the continent, such as in the Niger and Senegal River basins and at Lake Chad (Moreau 1967; Borrow & Demey 2001; Malling Olsen & Larsson 2004). This inland occurrence within Africa was explained by regular upstream movements along rivers (Borrow & Demey 2001; Malling Olsen & Larsson 2004). The occurrence close to water in Africa and movements along rivers illustrates the fact that large gulls are strongly tied to aquatic habitats (Malling & Olsen Larsson 2004). There is no evidence up to now for Lesser Black-backed Gulls crossing the interior of the Sahara by direct non-stop flights (Urban et al. 1986; del Hoyo et al. 1996; Borrow & Demey 2001). There exists a single ring recovery of an immature Lesser Black-backed Gull several hundred kilometres inland in the desert of Mauritania (Wernham et al. 2002).

Theoretical considerations suggest that Lesser Black-backed Gulls might have the potential to cross the Sahara by non-stop flights: Gulls are fast and tireless fliers and the possibility to use strong tailwinds would enable them to reach high migratory velocities (Liechti & Schaller 1999). If gulls could select such favourable winds, they would reduce the time of desert crossing to an extent that non-stop flights would become a realistic option.

Our observations demonstrate for the first time that trans-Sahara flights of Lesser Black-backed Gulls do in fact occur, that the birds fly at heights with tailwind support and low temperatures, and that the birds were only drifted by wind to a small extent.

Methods

Data were collected in Mauritania close to the oasis, Ouadâne, located about 500 km east of the Atlantic coast (20°56' N, 11°35' W). Ouadâne is situated at a transition of sandy to rocky desert about 420 m above sea level (asl). Radar observations were carried out from 06 March till 15 May 2003, from 24 August till 25 October 2003, and from 15 March till 10 May 2004, covering 22 hours per day. We used the tracking radar "Superfledermaus" to gather data on flight directions as well as on horizontal and vertical speed of roughly 17'400 bird targets per season (5'000 of them from diurnal migrants). If possible, birds tracked during daytime were identified visually through a telescope (12.4x, mounted parallel to the radar antenna). Wind measurements were conducted three times per day in 2003 and four times in 2004 up to an average height of 4.5 km asl. We calculated birds' heading and air speed by subtracting the wind vector from the bird's vector at the corresponding flight altitude (Bruderer 1994). For further information about the use of radar in ornithology see Bruderer (1997).

We present here data of identified flocks of large gulls. They could be determined by their slender, long-winged appearance, only slightly curved wings and constant wing flapping (with frequencies varying around 3 Hz). Two flocks consisted of adult Lesser Black-backed Gulls. In adult birds the dark upperwings flashed during the downstroke against the white underbody and bright sky. Another flock consisted of adults and immature Lesser Black-backed Gulls. The immature birds were characterized by their brown-greyish appearance. Other flocks could not be identified at the species level, because their upperwings were not seen. Since the Lesser Black-backed Gull is the only large gull species of the western Palaearctic wintering regularly south of the Sahara, we treat here all large gull observations together (Malling Olsen & Larsson 2004).

To estimate the temperature the gulls experienced during their flights crossing Ouadâne we downloaded air temperature data from the National Oceanic & Atmoshperic Administration (NOAA); NCEP/DOE AMIP-II Reanalysis (http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html). Data were available for morning (6am), midday (12 am) and evening (6 pm) at four different pressure levels (925 mbar, 850 mbar, 700 mbar, and 600 mbar) representing four altitude intervals (ground level – 1150 m, 1150 – 2400 m, 2400 – 4000 m, and 4000 – 5000 m). We interpolated the air temperature for the flight altitudes by using the temperatures at two pressure levels around gull's flight altitude. Statistics were calculated using the statistical software package R (R Development Core Team 2005).

Results

In spring six flocks (with 273 individuals) and in autumn two flocks (15 individuals) could be identified as large gulls with certainty (Tab. 1). Mean flight direction in spring was northeast (45° ± 11, n = 6, rho = 0.986), in autumn southwest (217° ± 17°, n = 2, rho = 0.844, Fig. 1) and mean flight speed 76 ± 21 km/h (sd, n = 6) in spring and 60 ± 18 km/h (sd, n = 2) in autumn, respectively. Vertical speed of all flocks was relatively low. Highest sinking rate was around 0.5 m per second. Considering only flocks that were recorded within two hours around a wind measurement, mean air speed over all seasons was 39 ± 6 km/h (sd, n = 5). Flight altitudes were similar between spring and autumn, between 2800 and 5100 m asl (Tab. 1). The flock tracked on 29 September 2003 in the early afternoon experienced the highest temperature of all flocks (13°C), and relatively low wind support.

Discussion

Lesser Black-backed Gulls crossed the desert oasis, Ouadâne, at high altitudes with (often strong) tailwinds and almost negligible drift by sidewinds. The mean air speed of 39 km/h corresponds well with air speeds (43-44 km/h) of other measurements of migrating Lesser Black-backed Gulls (Bruderer & Boldt 2001).

Flight directions were concentrated along a NE-SW axis, with headings equally concentrated along a NNE-SSW axis (Fig 1). This strongly indicates that the observed Lesser Black-backed Gulls were not accidentally drifted inland by the wind, but were on an intended migratory flight. If the Lesser Black-backed Gulls maintained their flight directions, the next marine habitats they might reach in spring would be the Mediterranean Sea (at a distance of about 2400 km, close to Algiers in Algeria) and in autumn the Atlantic coast of West-Africa (950 km, close to Dakar in Senegal; Fig. 1). With the measured seasonal mean flight speeds Lesser Black-backed Gulls would reach the suggested marine stopover sites within about 32- and 16-hour flights, respectively.

In total the gulls would fly presumably about 3300 km from the Atlantic to the Mediterranean Sea and vice versa. To cover successfully such a distance across the Sahara desert gulls have to increase their fat reserves, whether they fly non-stop or intermittently, because refuelling is largely impossible for wetland birds in the Sahara (Moreau 1961). Therefore, gulls have to carry a considerable extra weight. In Bar-tailed Godwits (*Limosa lapponica*) and Northern Wheatears (*Oenanthe oenanthe leucorhoa*) performing long non-stop flights (of several thousand kilometres) the fat load for migration was estimated to be about 40% (30-50%) of bird's lean body mass (Gill et al. 2005; Battley & Piersma 2005; Thorup et al. 2006). Wind-tunnel measurement with waders suggests that carrying such large reserves during non-stop flights may be cheaper than previously expected (Kvist et al. 2001). The interpretation for these unexpected findings by Kvist et al. (2001) is that either the metabolic power input being converted into mechanical power output may become more efficient with growing fuel load or the winglift coefficient might change by fuel load according to Rayner (2001). Furthermore, a migrant can minimize the amount of reserves required for migration by efficiently using the energy and water stores, i.e. fly where energetic and water costs are low. Wind is an important factor minimizing the energetic flight costs, e.g. Piersma & Jukema (1990), Butler *et al.* (1997), Liechti & Bruderer (1998), Green (2003) and Liechti (2006). All our observed gulls flew under tailwind conditions, some of them with wind support allowing them to double their migratory speed (Tab.1). Even higher values are reported by Liechti & Schaller (1999) for large migrating birds using low-level jet streams to speed up their migration over Israel. Extra energy might have been saved by migrating in formation flight, because this decreases the overall costs of migration compared with solitarily migrating birds (Lissaman & Schollenberger 1970; Hedenström & Alerstam 1995). In Greylag Geese (*Anser anser*) and Pink-footed Geese (*Anser brachyrhynchos*) about 3 to 5 % of the total flight costs were saved by flying in formation (Cutts & Speakman 1994; Speakman & Banks 1998).

In addition to energy saving, birds crossing deserts should carefully balance their water budget, since no water for refuelling is available (Klaassen 1996). For this purpose, birds should overfly the desert at high altitudes to minimize water expenditure in relatively cold and humid air. The gulls migrated at altitudes above 2800 m asl where temperatures were not higher than 13°C. In wind tunnel experiments the water efflux was relatively low in Red Knots (*Calidris canutus*) and Rose coloured Starlings (*Sturnus roseus*) below 15° C, but increased steadily at warmer ambient temperatures (Kvist 2001; Engel 2005). For pigeons Biesel & Nachtigall (1987) hypothesized, that the rate of water loss would be low enough for long-distance flight below 10°C.

We conclude that the gulls crossed the Western Sahara under relatively favourable atmospheric conditions with positive wind support and no indication for water stress. Assuming the same atmospheric conditions for the whole journey, a non-stop flight would last on average 50 hours, but ranging, according to the flight speeds, from 36 to 92 hours (Tab 1).

For Bar-tailed Godwits model predictions as well as the temporal and spatial distribution of sightings indicate that these relatively large waders perform extreme non-stop flights when crossing the ocean between Alaska and Australia (Gill *et al.* 2005; Battley & Piersma 2005). Also smaller birds, such as the Northern Wheatears are assumed to cross large ocean barriers by non-stop flights (Thorup *et al.* 2006). To cross the ocean from North America to the Caribbean and South America over distances of 3000 km, small migrants start with north-easterly winds in North America and climb up to 3000-6000 m south of Bermuda (Richardson 1976; Richardson 1980) and review by Williams & Williams (1990). In the semi desert of the Negev in Israel Bruderer (1994) observed that water- and wading birds (in contrast to passerines) continued their trans-desert migration into the morning at high altitudes. This was particularly pronounced when jet streams allowing extreme flight speeds to be reached (Liechti & Schaller 1999). For the Negev, the authors assumed that this behaviour indicates non-stop trans-desert migration of water- and wading birds.

Since there are practically no appropriated stopover sites for gulls in the Sahara, no tendencies of landing as indicated by low vertical speeds and – apart from one ring recovery (Wernham et al. 2002) – no ground observations available, we suggest that the Lesser Black-backed Gulls observed at Ouadâne performed up to 3300 km long non-stop flights across the Sahara, making use of favourable winds and low temperatures. An exceptional rainfall in autumn 2003 created ephemeral lakes in the vicinity of the observation site, where several wader and waterbird species were observed (Salewski *et al.* 2005). This indicates that these migrants cross the Sahara regularly (Moreau 1967), but land only if appropriate habitats occur. However, gulls were never recorded on the ground at such temporal lakes. The assumption of crossing the Sahara non-stop gets support from a satellite-tracked Lesser Black-backed Gull of the eastern subspecies (*L. f. fuscus*). Its locations received by the satellite suggest that the Lesser Black-backed Gull performed a 3100 km long non-stop flight along the Nile during its autumn migration (J. Kube pers. comm.).

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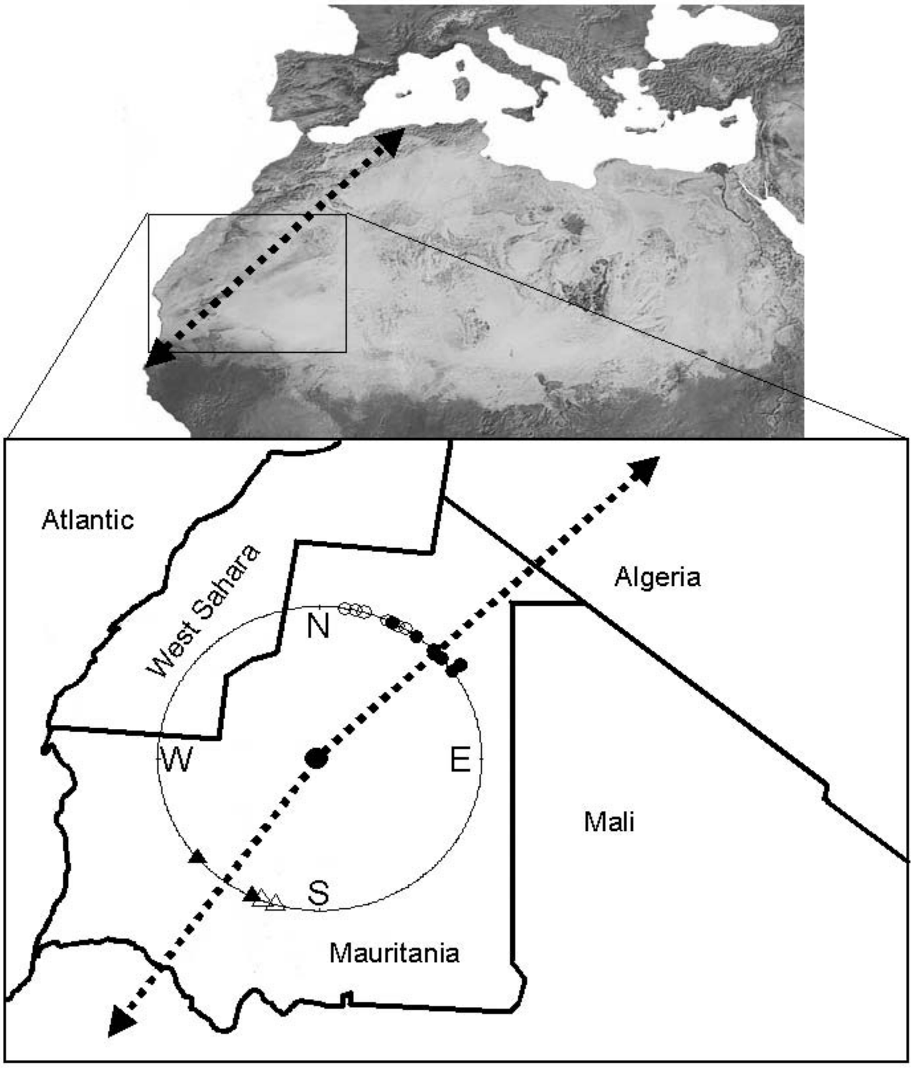
Table 1. Summary of visually identified Lesser Black-backed Gulls (*Larus fuscus*) and large gulls flying across Ouadâne, Mauritania. Mean time difference to nearest wind measurement (dtW) is given to evaluate the air speed information appropriately.

Taxon	Number	Date	Time	Altitude asl [m]	Flight dir. [°]	Heading [°]	Wind dir. [°]	Flight speed [km/h]	Air speed [km/h]	Wind speed [km/h]	Vertical speed [m/s]	dtW [min]	remarks
L. fuscus	70	04.4.03	14:53	5054	54	25	294	75	65	37	-0.06	250	2/3 ad.
L. fuscus	110	16.4.03	08:13	3950	27	16	245	36	30	8	-0.26	65	all ad.
large gulls	3	02.4.04	10:36	4228	54	29	253	92	43	56	0.08	30	-
L. fuscus	80	08.4.04	07:36	3350	46	13	251	77	38	50	0.13	120	-
large gulls	8	27.4.04	06:35	3341	49	32	244	83	41	46	0.24	59	all ad.
large gulls	2	27.4.04	07:43	4363	37	9	252	92	59	49	-0.46	127	-
large gulls	5	31.8.03	16:39	4555	229	201	82	72	44	39	-0.43	99	-
large gulls	10	29.9.03	14:29	2869	205	196	52	47	36	12	-0.61	217	-

Figure 1. Flight directions of large gulls crossing the oasis Ouadâne (Mauritania). The upper map provides an overview of North-Africa and South-Europe. Dotted arrows indicate on both maps mean flight directions for spring and autumn at Ouadâne (black dot). Single flight directions (filled symbols) and headings (open symbols) of gull flocks are shown in the graph below. Circles refer to spring (flight direction: 45° ± 11, n = 6, rho = 0.986; heading: 21° ± 9°, n = 6, rho = 0.989) and triangles to autumn (flight direction: 229° and 205°, rho = 0.978; heading: 201° and 196°, rho = 0.999) migration. “rho” is the sample mean resultant length.



VIII

VIII SYNTHESIS AND OPEN QUESTIONS

Several billion migrants cross the Sahara twice a year. We chose radar to collect data about bird migration and applied a new method to quantify passerine migration. Its temporal pattern proves that the intermittent migration is the predominant flight strategy to cross the Sahara with massive take-off after sunset, persistent migration throughout the night and a density decrease after sunrise. During nighttimes passerine's altitudinal distribution was governed by the wind conditions and not by water costs.

Method

We developed for the first time a method to transform radar data into true numbers of birds aloft. However, we are still far away from an easily applied process of bird quantification, because echoes must be identified individually by an expert and the quantification method can only be applied when birds are flying singly (see below) .

Although birds and insects differ in their echo signatures (amplitude variation of echo size over time) and standardized echo sizes, we failed to find an algorithm for an automatic bird-insect identification. Until now each echo has to be classified visually by the echo signature. For this discrimination, expert knowledge is required. However, even experts may not assign borderline echoes between birds and insects always in the same way. An automatic differentiation between these most abundant radar echoes would be very welcome to standardize and speed up echo identification.

Passerine migrants fly solitarily during nighttimes. At least over the western Sahara nighttime migration densities are rather low (about < 1 passerine per km^3). This suggests that flocking of nocturnal passerines prolonging their migratory flights into the day is not a frequent event. This reasoning is supported by observations through the telescope mounted parallel to the optical axis of the radar antenna: We only rarely observed passerine flocks (swallows excluded) during the day. However, swallows, swifts, water- and wading birds cross the western Sahara often in flocks during the day. In flocks the reflected energy of the different birds interfere and consequently do not produce a typical echo signature of the bird guild involved. Therefore, flocks detected by radar alone cannot be classified on the bird guild level, i.e. passerine -, swift - and wader-types and cannot easily be quantified with respect to bird number.

The method for quantification presented in this thesis is the most advanced procedure of quantification and seems to be well adjusted to nocturnal migration, but it holds some disadvantages when flocks are involved. Therefore, we quantified only passerine migration and did not investigate quantitatively migration strategies of other bird guilds flying often in flocks.

Migration strategies

Non-stop or intermittent migration?

Passerines cross the Sahara desert predominately by an intermittent flight strategy. At all sites some passerines prolonged their migratory flights far into the day. On the one hand passerines used strong tailwinds during the mornings to speed up their migratory velocity and on the other hand passerines, especially at the desert sites, might perform daytime flights in search of suitable daytime stopover sites within the bare sand desert.

On some mornings, when passerines prolonged their migratory flights using favourable winds, migrants experienced flight speeds ranging up to 100 or even 140 km/h. Assuming a four hour flight they would cover about 400 to 560 km. A bird in such a fast flight would cover the full distance of a normal night-flight with 50 km/h in just four hours. This explains the advantage a migrant gains by switching from typical intermittent migration to prolonged flights. Since we do not find a time lag in the daytime migration pattern of nocturnal migrants between Ouadâne and Bîr Amrâne, only a small proportion of passerines may migrate actually non-stop. However, about 10% of the whole passerine migration occurred during the afternoons at these both sites in spring. It seems that some passerines continued their migratory flight throughout the whole day, but for how long these few daytime flights really last cannot be answered with our data.

Prolonged migratory flights may also be understood as explorative movements to find a “suitable” resting site, especially at the desert sites. Passerines flying over the bare sand desert may have a high motivation to carry on flying for some time even after sunrise to find a shadowed place for the daytime stopover. In the vicinity of the two desert sites only some small plants spent little shade. During the whole day, especially in the mornings, new passerines arrived at the desert sites and selected shadowy places for their daytime stopover. All birds were caught and ringed. Only ten out of 179 passerines (wagtails and pipits being mostly diurnal migrants were excluded) did not depart during the subsequent night. Most passerines were in good body condition, 162 had a muscle score larger than one and 137 had a fat class higher than two. This arrival-departure pattern and the body condition of the birds indicate that these birds are not fallouts, but that most of them are due to finish successfully their migration across the Sahara.

The biologically important strategy of passerines to cross the Sahara is clearly the intermittent migration. Even if non-stop migration is performed by some passerines, its proportion is very low because of the massive take-off even in the bare sand desert after sunset. True non-stop migration is only of minor importance. However, as there are only a few oases serving as energy and water refuelling sites within the Sahara, most passerines fly the whole distance across the Sahara non-stop in terms of nutrition.

In contrast to the intermittent migration of passerines Lesser Black-backed Gulls (*Larus fuscus*) may serve as one example from the wetland-dependent group of the Laro-Limicolae, which most probably cross the western Sahara by a long non-stop flight. Most likely this non-stop flight strategy is also shown by water- and shorebirds possessing similar flight abilities and being only rarely observed on the ground in contrast to high numbers passing aloft. Until now we failed to properly quantify water- and shorebird migration, because many flocks were involved. However, by using mean number of birds of visually identified flocks and echo expansions there might be a chance to approximate flock quantification in the future.

Minimization of water or energy?

Bird’s flight range is, simplified, determined by bird’s body condition, but its limit is modulated by meteorological conditions, mostly wind, temperature and humidity. Nocturnal flights occur at altitudes with best wind support, as demonstrated by autumn passerine altitudinal distribution. 90% of the passerines migrated where good wind prevailed in spite of high water costs due to ambient temperatures of often more than 30° C. In autumn passerine migration was more restricted to nighttimes than in spring when migration occurred at higher altitudes. We hypothesize that autumn passerines experience higher water (warm temperatures and intensive solar radiation) and energy (air turbulences) flight costs at low altitudes during the day than spring migrants higher up. Therefore, fewer passerines continue their migration into the day in autumn than in spring. We, furthermore, assume that passerines migrate intermittently due to the high flight costs with respect to water and energy consumption during the day. Since daytime passerine migration is rather low in the western Sahara, it is difficult to find out why they rarely migrate during the day. In wind tunnels temperature, solar radiation and turbulences can be modified independently of each other. Passerines can be exposed to a variation of these three factors during flight and flight costs under different conditions can be determined. For instance, flying at high temperatures but being not exposed to solar radiation might be cheaper than flying at the same temperature and intensive solar radiation, which might heat up the bird additionally. Such experiments may help to identify the reasons why passerines migrate usually only during nighttimes.

Due to the intensive take-off after sunset, high flight altitudes during the night and an increasing density of passerines at lower altitude towards dawn in spring, we assume that passerines migrate on average for nearly the entire night. However, we cannot exactly determine with our radar data for how many hours passerines fly during one flight step. As birds trained to fly in wind tunnels refuse to do so at temperature of more than 25° C, and calculations derived from wind tunnel experiments indicate that birds would be dehydrated after two flight hours at more than 25° C, one may wonder for how long passerines are capable of flying under the extreme autumn conditions in the Sahara. In the near future satellite transmitters may be small enough to track passerines. This might provide a new chance to follow individual passerines during their migration and derive information not only about the flight duration of single migration steps, but also about their precise migratory route, the time required for the Sahara crossing and wintering sites.

IX

IX Summary

The aim of this thesis was to investigate the flight and resting strategies of birds crossing the Sahara on migration. In order to overcome the severe limitations of ground observations, we chose radar to obtain continuous data of the temporal and spatial distribution of bird migration and to answer the core question whether migrants cross the largest desert by a long non-stop flight or rather by intermittent flying and resting.

Study site and methods

The Swiss Ornithological Institute carried out extensive radar and field studies at three different study sites in Mauritania, covering three migration seasons in 2003 and 2004. One station (20°56’ N; 11°35’ W), close to the oasis Ouadâne and about 500 km east of the Atlantic coast, was run permanently for about two moths in spring and autumn 2003 and in spring 2004. It provided continuous data on the course of bird migration across this part of the Sahara. The two other radar sites were operated about 300 km further to the East in the plain sand desert close to the border of Mali. At Mohammed Lemna (18°35’ N; 08°38’ W) radar data was collected for eleven days in September 2003. At Bîr Amrâne (22°47’ N; 08°43’ W), located about 450 km further to the North of Mohammed Lemna, the observations covered about three weeks in April 2004 (**chapter I**).

Quantification of bird migration by means of radar is still a difficult task, in spite of almost sixty years of growing experience in radar ornithology. We present for the first time a method how radar data can be analysed to achieve reliable estimates of the number of migrating birds in a given air space. To reach this goal three basic steps of quantification must be considered: (1) echo detection, (2) echo identification and (3) quantification. First, the radar must be calibrated to allow the calculation of standardized echo sizes that are independent of distance. Then a distance-dependent threshold to reduce the detection of small targets at close range has to be applied. After this basic step, the remaining echoes must be assigned to bird or insect targets, eventually eliminating the insects. In our case, we were also able to determine the birds’ body axis relative to the radar (aspect) and to differentiate detection probabilities according to echo sizes. For the final quantification, we estimated the surveyed air space with respect to the specific detection range per echo size class. Using this method we calculated the temporal and spatial distribution of bird migration crossing the western Sahara (**chapter II**).

Composition of daytime migration

Billions of songbirds breeding in the western Palaearctic cross the Sahara desert twice a year. While crossing temperate latitudes most of them use an intermittent flight strategy, i.e. fly at night and rest or feed during the day. As resting and feeding in the Sahara is much less rewarding than in Europe, we investigated whether in the Sahara migration during daytime comprises the normal diurnal migrant species or the nocturnal ones prolonging their flight into the day.

At the radar station Ouadâne, spring passage of passerine migrants showed high variation from night to night, but in general passerine densities decreased towards sunrise. However, under favourable wind conditions passerine migration continued far into the day, mostly at high altitudes (around 2000 m above ground level). These relatively high densities of passerines flying during the day were in contrast to very low proportions of real diurnal migrants detected on daily transect counts in the study area. For nocturnal migrants, however, the transect counts showed high correlation

with nocturnal passage of passerine migrants. The conclusion is that most of the recorded daytime migration (aerial hunters and soaring birds excluded) consisted of nocturnal passerine migrants prolonging their migratory flights far into the day under favourable wind conditions. Furthermore, we hypothesize that individual birds have the choice to restrict migration to nighttimes or, alternatively, to extend their flights into the day, suggesting that flexibility is the main strategy (**chapter III**).

Non-stop or intermittent migration

For a long time the standard assumption was that passerines overcome the Sahara in a 40 hours non-stop flight. However, ground observations of passerines resting in good body condition in the Sahara indicated that at least some migrants used an intermittent strategy. In order to estimate the proportions of non-stop and intermittent passerine migration across the Sahara, we quantified passerine migration with radar at all three study sites during spring and autumn migration.

During spring the last main stopover area before the desert-crossing is the Sahel savanna. Non-stop flying birds taking off around sunset in the northern Sahel and flying with 50 km/h would reach Ouadâne not before 2 am. The last birds passing the Sahel-Sahara boundary around 4 am would pass the oasis at around 11 am. The same hypothetic non-stop wave would reach the desert site (Bîr Amrâne, about 200 km further north) four hours later. Thus, if passerines migrate non-stop we would expect a time lag between the wave at Ouadâne and Bîr Amrâne of about four hours. In autumn, major departure areas in the Atlas Mountains would allow the first songbirds to reach Ouadâne around midday, and last birds of the non-stop wave would have passed the oasis by 10 pm. As Mohammed Lemna lies about 270 km further inland and 250 km further south than Ouadâne, we assume that the hypothetic non-stop wave would fly over this site from 7 pm until 4 am.

Massive departure of passerines just after sunset and persistent migration through the whole night independent of site and season indicate that take-off took place in the vicinity of the study sites. Thus, songbirds have rested in the desert during the day. This rejects the non-stop and verifies the intermittent hypothesis. Daytime migration was more pronounced in spring than in autumn. The majority of this daytime passage was not part of a non-stop wave crossing Ouadâne and subsequently Bîr Amrâne, because passerine densities decreased considerably after midday when still migration should occur according to the non-stop hypothesis at Bîr Amrâne (**chapter IV**).

Minimization of energy or water consumption

Passerines store fat and protein before they encounter ecological barriers. During the crossings energy and water consumption is influenced by atmospheric conditions, such as wind, air turbulences (for energy expenditure) and air temperature, oxygen concentration and relative humidity (for water expenditure). As these meteorological factors change in time and space (mainly altitude) birds can minimize their energy or water consumption by selecting best times and altitudes for migration. The majority of passerines migrate intermittently across the Sahara (**chapter IV**) choosing nighttimes for flying. With respect to flight altitudes, the question arises whether a passerine selects a certain altitude to minimize energy or water consumption. We used a physiological model to predict the flight ranges in respect of the energy and water consumption for different flight altitudes. These daily altitudinal predictions were compared with the altitudinal distribution of passerines measured by radar.

In spring, nocturnal passerines appear to migrate mostly at altitudes, where the energy expenditure can be minimized, but predictions of the energy- and water/energy-models did not differ significantly (**chapters V and VI**), because minimal energy and water consumption occurred within the same altitude ranges. In contrast, autumn migrants face a trade-off between favourable winds with hot and dry air at low altitudes and humid and cold air combined with unfavourable winds higher up. Thus, birds can either minimize their water consumption by flying at high altitudes or speed up their migration by using tailwinds close to the ground. In autumn nearly 90% of the nocturnal songbird migration occurred at low altitudes (<1000 m above ground level). Songbirds experienced there at least 30°C and only 30% relative humidity. The flight altitude of nocturnally migrating songbirds was highly predicted by the wind distribution, but not by water consumption suggesting that water stress is not an important factor during nocturnal flights (**chapter VI**).

Since daytime migration of passerines was rather low, we could not statistically analyse the model predictions and passerines altitudinal distributions. Circumstantial evidence suggests, however, that a combination of high energy demand (due to air turbulences) and water consumption (due to warm, dry air and solar radiation) during daytime flights may prevent songbirds from prolonging their nocturnal flights regularly into the day (**chapter VI**).

Non-stop Sahara crossing of Lesser Black-backed Gulls

The Lesser Black-backed Gull (*Larus fuscus*) is the only large gull from the western Palaearctic wintering regularly in sub-Saharan Africa. This species uses either coastlines or the Nile valley to reach its wintering grounds in Africa. Rare inland observations at wetlands within Africa were explained by regular upstream movements along rivers. At Ouadâne we observed for the first time several flocks of Lesser Black-backed Gulls and large gulls of probably the same species crossing the western Sahara. Mean flight direction was in spring 45° ± 11 (sd, n = 6) and 229° and 205° for two autumn flocks. Thus, flight directions (with minimal side wind) were relatively concentrated along a northeast–southwest axis indicating that the observed gulls were not accidentally drifted inland by wind, but were on intended migratory flights. Flocks flew at a mean altitude of 3500 ± 730 m (sd, n = 8). Some groups migrated under strong tailwind conditions and reached high flight speeds of up to 90 km/h. It seems that gulls migrated under favourable conditions in respect of the water and energy consumption suggesting strongly that they performed long non-stop flights between the eastern Atlantic coast and the Mediterranean Sea (**chapter VII**).

IX ZUSAMMENFASSUNG

Das Ziel dieser Dissertation war es, die Flugstrategie der Zugvögel bei der Sahara-Überquerung zu erforschen. Nur anhand von Bodenbeobachtungen ist es extrem schwierig und unsicher auf das tatsächlich ablaufende Zuggeschehen in der Luft zu schliessen. Daher quantifizierten wir die räumliche und zeitliche Verteilung des Vogelzuges mittels Radar. So liess sich zum ersten Mal klären, ob Zugvögel die Sahara in einem langen Non-Stop-Flug oder mit einer intermittierenden Zugstrategie, Flug in der Nacht und Rast am Tag, überqueren.

Radarstandorte und Methode

Die Schweizerische Vogelwarte führte eine umfassende Radar- und Felduntersuchung an drei verschiedenen Orten in der westlichen Sahara, Mauretanien, während drei Zugperioden (Frühling und Herbst 2003 sowie Frühling 2004) durch. Die Hauptstation befand sich in der Nähe der Oase Ouadâne (20°56’ N; 11°35’ W) etwa 500 km östlich der Atlantikküste und wurde während der drei Feldsaisons je für zwei Monate permanent betrieben. Die beiden anderen Radarstandorte lagen etwa 300 km weiter östlich als Ouadâne in der Sandwüste nahe der Grenze zu Mali. In Mohammed Lemna (18°35’ N; 08°38’ W) wurde der Vogelzug während elf Tagen im September 2003 und in Bîr Amrâne (22°47’ N; 08°43’ W) 450 km nördlich von Mohammed Lemna über einen Zeitraum von ungefähr drei Wochen im April 2004 quantifiziert (**Kapitel I**).

Die Quantifizierung des Vogelzuges mittels Radar ist trotz der 60-jährigen Erfahrung im Bereich der Radarornithologie immer noch eine sehr schwierige Aufgabe. Wir stellen hier zum ersten Mal eine Methode vor, mit welcher Radardaten so analysiert werden können, dass die Anzahl ziehender Vögel in einem bestimmten Volumen zuverlässig geschätzt werden kann. Um das zu erreichen, müssen drei grundlegende Schritte der Quantifizierung berücksichtigt werden: (1) Echodetektion (2) Echoidentifizierung und (3) Quantifizierung. Zuerst muss der Radar kalibriert werden, damit standardisierte Echogrössen, die dann distanzunabhängig sind, berechnet werden können. Erst danach kann eine distanzabhängige Schwelle, um die vermehrte Detektion von kleinen Zielen (hauptsächlich Insekten) in geringer Distanz zum Radar zu reduzieren, sinnvoll angewendet werden. Schliesslich müssen die verbleibenden Echos auf dem Vogel-Insekt-Niveau bestimmt werden, um letztendlich die Insekten auszuschliessen. Weiterhin muss die Lage der Körperachse des Vogels relativ zum Radar bestimmt und zwischen den Detektionswahrscheinlichkeiten der verschiedenen Echogrössen unterschieden werden. Für eine verlässliche Quantifizierung muss zudem der überwachte Raum bezüglich der spezifischen Detektionsreichweite pro Echogrösse geschätzt werden. Mithilfe dieser Quantifizierungsmethode wurde die zeitliche und räumliche Verteilung des Singvogelzuges über der westlichen Sahara bestimmt (**Kapitel II**).

Zusammensetzung des Tagzuges

Vier Milliarden Singvögel, die in der Westpaläarktis brüten und südlich der Sahara überwintern, überqueren zweimal im Jahr die Sahara. In den Gemässigten Breiten ziehen diese Singvögel intermittierend, d.h. sie fliegen in der Nacht und rasten oder fressen am Tag. Da sich dieses Verhalten aufgrund der unwirtlichen Bedingungen am Boden in der Sahara sehr viel weniger lohnt als in Europa, überprüften wir, ob der Tagzug in der Sahara hauptsächlich aus „echten“ Tagziehern besteht, oder ob eigentliche Nachtzieher ihren Flug nicht zu einem gewissen Teil in den Tag hinein verlängern.

Zwar variierte der Frühlingszug der Singvögel recht stark von Nacht zu Nacht in Ouadâne, doch nahm die Zugintensität nach Sonnenaufgang im Allgemeinen deutlich ab. Herrschten jedoch günstige Winde vor, so verlängerten viele Singvögel ihren Zug weit in den Tag hinein. Diese relativ hohen Tagzugdichten standen im deutlichen Gegensatz zu den sehr wenigen „echten“ Tagziehern (Lerchen, Stelzen und Pieper), die wir während der täglichen Transektzählungen in unserem Untersuchungsgebiet beobachteten. Die Bodendichten der Nachtzieher korrelierte hingegen signifikant mit den nächtlichen Durchzugszahlen der Singvögel. Daher gehen wir davon aus, dass der am Tag registrierte Vogelzug (Schwalben, Segler, Spinte und Seglerflieger ausgeschlossen) hauptsächlich aus eigentlichen Nachtzieher besteht, die ihren Zug bei günstigen Winden in den Tag hinein verlängern. Singvögel haben also die Wahl zwischen einer nur auf die Nacht beschränkten oder auf den Tag ausgedehnten Flugstrategie (**Kapitel III**).

Non-Stop oder intermittierender Zug

Sehr lange wurde vermutet, dass Singvögel die Sahara in einem ununterbrochenen 40 Stundenflug überqueren würden. Nachdem jedoch Singvögel in der Sahara in einem guten Körperzustand gefangen worden waren, deutete vieles daraufhin, dass zumindest einige Singvögel die Wüste mit einer intermittierenden Flugstrategie überqueren. Um den Anteil von Non-Stop und intermittierendem Zug von Singvögeln über der Sahara abzuschätzen, quantifizierten wir den Singvogelzug an allen drei Radarstandorten während des Frühling- und Herbstzuges.

Im Frühling liegen die letzten Hauptrastgebiete vor der Sahara-Überquerung in der Sahel-Savanne. Da Singvögel in der Regel kurz nach Sonnenuntergang aus den Rastgebieten abziehen, würde man bei Non-Stop-Ziehern, die vom nördlichen Rand des Sahel abziehen, erwarten, dass sie Ouadâne nicht vor 2 Uhr nachts erreichen, wenn man die durchschnittliche Fluggeschwindigkeit von 50 km/h annimmt. Die letzten Vögel einer solchen Non-Stop-Welle, die den Sahel-Sahara-Rand gegen 4 Uhr morgens überqueren, würden die Oase gegen 11 Uhr mittags überfliegen. Die selbe hypothetische Non-Stop-Welle würde Bîr Amrâne, 200 km nördlich von Ouadâne gelegen, vier Stunden später passieren, das Ende der Welle also gegen 15 Uhr nachmittags. Falls Singvögel non-stop ziehen, dann würden wir einen zeitlichen Abstand von vier Stunden in den Durchzugsmustern der Non-Stop-Wellen von Ouadâne und Bîr Amrâne erwarten. Im Herbst befinden sich die letzten wichtigen Rastgebiete vor der Sahara-Überquerung in dem Atlas-Gebirge, und die ersten Singvögel einer Non-Stop-Welle würden Ouadâne mittags und die letzten gegen 22 Uhr abends überfliegen. Da Mohammed Lemna 270 km weiter östlich und 250 km weiter südlich von Ouadâne gelegen ist, nehmen wir an, dass die hypothetische Non-Stop-Welle diesen Wüstenstandort zwischen 19 und 4 Uhr morgens überqueren würde.

Intensiver Aufbruch von Singvögeln nach Sonnenuntergang, anhaltender Singvogelzug während der gesamten Nacht und reduzierter Zug nach Sonnenaufgang unabhängig vom Ort und von der Saison zeigen deutlich, dass der Singvogelabzug aus der Nähe der Radarstandorte erfolgt ist. Folglich haben die Singvögel den Tag über in der Wüste gerastet. Dies widerlegt klar die Non-Stop- und bestätigt die Hypothese, dass Singvögel mit einer intermittierende Zugstrategie die Wüste überqueren. Der Singvogeltagzug war im Frühling deutlicher ausgeprägt als im Herbst. Die Mehrheit des Tagzuges war allerdings nicht Bestandteil einer Non-Stop-Welle, die zuerst Ouadâne und später Bîr Amrâne überflog. Die Singvogeldichten reduzierten sich deutlich gegen Mittag an beiden Orten, wenn eigentlich nach der Non-Stop-Hypothese noch Singvogelzug bis in den Nachmittag in Bîr Amrâne erwartet worden wäre. So werden die meisten tagziehenden „Nachtzieher“ wohl gute Winde ausgenutzt haben, um ihren Zug in den Tag hinein zu verlängern aber nicht um non-stop zu ziehen (**Kapitel IV**).

Minimierung von Energie- oder Wasserverbrauch

Singvögel legen Fett- und Proteinreserven an, bevor sie ökologische Barrieren überqueren. Der Energie- und Wasserverbrauch während einer solchen Überquerung ist stark von den atmosphärischen Bedingungen beeinflusst; Wind und Luftturbulenzen bedingen die Energie- und Lufttemperatur, Sauerstoffgehalt sowie relative Feuchte die Wasserkosten. Da sich diese meteorologischen Parameter in Zeit und Raum (hauptsächlich Höhe) verändern, kann ein Vogel seinen Energie- und Wasserverbrauch minimieren, indem er die günstigste Zeit und Flughöhe für den Zug auswählt. Die Mehrheit der Singvögel zieht intermittierend über die Sahara und fliegt dabei nachts (**Kapitel IV**). Es stellt sich nun die Frage, ob die Zugvögel ihre Flughöhe aufgrund des Energie- oder Wasserverbrauchs auswählen. Mithilfe eines physiologischen Modells berechneten wir die günstigsten Flughöhen in Abhängigkeit von den Energie- und Wasserkosten für verschiedene Höhenbereiche. Diese Flughöhenvorhersagen verglichen wir dann mit den gemessenen Höhenverteilungen der Singvogeldichten.

Es scheint, dass Singvögel im Frühling in solchen Höhen fliegen, in welchen die Energieausgaben minimiert werden können. Allerdings unterscheiden sich die Energie- und Wasser-Modelle nicht signifikant voneinander (**Kapitel V und VI**), weil die Flugkosten bezüglich der Energie und des Wassers in denselben Höhenbereichen minimal waren. Im Herbst ergibt sich für die Zugvögel bezüglich der Flughöhenwahl jedoch ein Konflikt. In Bodennähe herrschen günstige Winde mit heisser und trockener Luft, während weiter oben sehr ungünstige Winde aber mit kalten, relative feuchten Luftmassen wehen. Folglich können Singvögel entweder ihren Wasserverbrauch minimieren, indem sie in grossen Höhen fliegen oder sie können ihre Zuggeschwindigkeit maximieren, wenn sie die vorteilhaften Winde in Bodennähe auswählen.

Fast 90% des nächtlichen Herbstzuges erfolgten in den unteren 1000 m, wo Temperaturen von über 30°C in sehr trockener Luft (<30% Feuchte) vorherrschten. Die Flughöhe der nachtziehenden Singvögel wurde sehr genau durch die Windverteilung und nicht durch den Wasserstress vorhergesagt (**Kapitel VI**).

Der schwach ausgeprägte Tagzug liess keine statistische Auswertung der Modellvorhersagen und Singvogelhöhenverteilung zu. Dennoch vermuten wir, dass ein Zusammenspiel von hohen Energie- (Luftturbulenzen) und Wasserkosten (warme, trockene Luft und Sonnenstrahlung) eine regelmässige Verlängerung des Zuges in den Tag hinein verhindern (**Kapitel VI**).

Non-stop Saharaüberquerung von Heringsmöwen

Heringsmöwen (*Larus fuscus*) sind die einzigen Grossmöwen der Westpaläarktis, die regelmässig südlich der Sahara überwintern. Sie ziehen entweder entlang der Küsten oder des Nils in ihre afrikanischen Überwinterungsgebiete. Sehr selten werden Feuchtgebiete im Inneren Afrikas aufgesucht. Zu diesen gelangen sie, wenn sie Flüssen stromaufwärts folgen. Wir beobachteten mehrere durchziehende Trupps von Herings- sowie Grossmöwen (wahrscheinlich ebenfalls Heringsmöwen) in Ouadâne. Ihre durchschnittliche Flugrichtung im Frühling betrug 45° ± 11 (sd, n = 6). Die beiden Herbstschwärme flogen in südwestliche Richtung (229° und 205°). Die Flugrichtungen konzentrierten sich also relativ stark entlang einer NE-SW-Achse, was daraufhin deutet, dass die Möwen nicht zufällig landeinwärts verdriftet worden waren, sondern sie sich auf einer beabsichtigten Flugroute befanden. Die mittlere Flughöhe war mit 3500 ± 730 m (sd, n = 8) über Meereshöhe relativ hoch, und die wärmste erfahrene

Lufttemperatur über Ouadâne lag bei nur 13°C. Einige Trupps zogen bei sehr starken Rückenwinden und erreichten Fluggeschwindigkeiten von über 90 km/h. Die Möwen sind also unter günstigen Bedingungen hinsichtlich des Wasser- und Energieverbrauchs über die westlichen Sahara gezogen. Wir vermuten daher, dass Heringsmöwen lange Non-Stop-Flüge zwischen der östlichen Atlantikküste und dem Mittelmeer durchführen (**Kapitel VII**).

X

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XI

XI CURRICULUM VITAE

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Born	10th January 1974 in Kiel, Germany
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EDUCATION

1980 – 1994	High-school-leaving certificate at the Max-Planck Schule, Kiel, Germany
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1998 – 1999	Visiting student at the biology department of the University of York by the means of a DAAD scholarship, England
1999 – 2002	University degree in biology with major course zoology, minor courses botany and conservation at the Georg-August University of Göttingen, Germany Diploma thesis *Untersuchungen zu den Optimalitätskriterien rastender Singvögel während des Wegzuges: Minimieren Steinschmätzer Energie, Zeit oder Prädationsrisiko?* Supervision: Prof. Dr. Matthias Schaefer, Dr. Volker Dierschke
2002 – 2006	Dissertation at the Swiss Ornithological Institute, Sempach, and the University of Basel, Switzerland *The relative importance and biological significance of non-stop and intermittent flight strategies in bird migrants crossing the Sahara.* Supervision: Prof. Dr. Bruno Bruderer, Dr. Felix Liechti
2005 – 2007	Advanced study in applied statistics at the Swiss Federal Institute of Technology Zurich, Switzerland. Supervision: Prof. Dr. Werner A. Stahel

PRACTICAL TRAINING

1996	Voluntary work at the National Nature Reserve Gibraltar Point, Yorkshire, England, for three months; including management/conservation work, project of protection of endangered species (*Bufo calamita*), ornithological surveys
2000	Voluntary work at the national park Jasmund on the island Rügen, Mecklenburg-Vorpommern, Germany, for two months; leading the ornithological training of the rangers

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2002	Scientific assistant in a field project about stopover ecology of Northern Wheatears (*Oenanthe oenanthe*) under supervision of Dr. V. Dierschke at the Institut für Vogelforschung, “Vogelwarte Helgoland”, Schleswig-Holstein, Germany, for three months
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Founded in 1924 and situated on the shores of Lake Sempach near Lucerne, the Swiss Ornithological Institute is a private foundation for ornithological research and conservation. Initially a ringing centre, it nowadays covers a wide range of topics from bird migration and avian ecology to population monitoring and nature conservation. It further accommodates one of Europe's most important ornithological libraries. Some recent projects were aimed at ecophysiology of migrating birds, moulting patterns of passerines, the breeding bird atlas for Switzerland, and behavioural ecology of various species. Focal points of the institute's tasks are: Continuous monitoring of populations and distributions combined with periodic reports on the situation of the avifauna, phenology of breeding and migration in relation to climate, population ecology as well as conservation projects and landscape management.

Studies on bird migration have been a priority in the institute's work since its beginnings. During the last 35 years, adaptations of migratory birds to meteorological and ecological factors have been studied by various methods including tracking radar, infra-red camera and moon-watching as well as mist-netting and banding combined with physiological studies at different sites. Since the early 1970's migration across the Alps has been investigated. In 1991 and 1992 the Swiss Ornithological Institute conducted a research project in the Negev Desert in southern Israel on the weather dependence of directions, speeds, and altitudes of nocturnal migrants and on flight behaviour of soaring migrants. In 1996 and 1997 a project in the western Mediterranean area investigated the proportion of long distance migrants crossing the western Mediterranean and the Iberian Peninsula, and the importance of land bridges and islands for the Western Palaearctic bird migration system. In 2003 and 2004 an extensive bird migration project was carried out in the southwestern Sahara, Mauritania, to investigate flight strategies of trans-Sahara migrants crossing this vast ecological barrier during spring and autumn migration. In the main focus were quantification of bird migration, flight direction and altitudes, and stopover behaviour of nocturnal songbird migrants.

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