Concluding remarks

The relevance of taking into account site-specific habitat and geographic characteristics

Wet *versus* dry Balearics

Of the 23 species for which enough data was available, in 18 (78%) mean body mass was significantly higher (in one nearly so) in the wet Balearics than in the dry Balearics (a similar result was obtained when analysing only data from common years; significant differences being found in 10 out of 13 species). These differences were generally paralleled by fat stores and physical condition and indicate that in general birds trapped in the wet Balearics were clearly in better average condition than those from the dry Balearics. Overall, average body mass across species was *c.* 7% lower in birds trapped in the dry Balearics, a relevant difference if we bear in mind, for example, that average body mass in the dry Balearics is only *c.* 4% lower than in Catalonia (table 1). In three species (Sedge and Garden Warblers and Pied Flycatcher) differences in body mass were also paralleled by differences in third primary and wing lengths, which in the wet Balearics were significantly longer in these three species than in the dry Balearics.

The present findings suggest that the dry Balearic sites attract birds that are on average in poorer body condition and thus are more likely to stop at the first opportunity. The fact that in some species the birds trapped in the dry Balearics had shorter wings also corroborates this view, since smaller size and/or shorter wings imply poorer flight capacity and higher susceptibility to adverse weather conditions (*cf.* Newton, 2008; Saino et al., 2010), which in turn lead to greater energetic stress levels. The frequency distribution of body mass, exemplified here by the Willow Warbler and the Common Swallow, indicates that the degree of variability is quite similar in both areas, although with on average lower values on dry islands (fig. 1). Thus, rather than a lack of captures of fat birds in less suitable stopover areas, the differences revealed here seem to reflect that the leaner is the bird the higher is its tendency to land at the first available site.

In contrast to the wet Balearics, the dry Balearic sites are located in smaller and more isolated islands and in more sparsely vegetated and less productive habitats. These sites, therefore, are not optimal for recovering from long flights and offer poor refuelling opportunities for forest and wetland species. Their lower suitability is further highlighted by the fact that in birds trapped here body mass at first capture tended to be clearly lower in birds retrapped on subsequent days than in those trapped only once (significantly so in 16 out of 29 species), an indication that birds that select to stay tend to be in poorer body condition and have less capacity to search for better areas. Moreover, those staying usually had negative fuel deposition rates (significantly so in 11 out of 29 species).

Given the great differences in habitat suitability between the dry and wet Balearics, it seems reasonable to assume that –whenever possible– birds will try to select the best stopover areas; it is well-known that migrants select with precision prior to or during landfall the habitats of their stopover sites (Chernetsov, 2006). In the Balearics (but apparently also elsewhere) this phenomenon is probably facilitated by the fact that landing seems to occur largely at dawn or shortly afterwards (Bruderer et al., 1996; Liechti et al., 1997; Chernetsov, 2006). Nevertheless, the question remains as to why better and not poorer body condition should lead to select for more suitable sites. Birds in poorer condition have greater need to refuel and thus may be more urged to select good quality stopover areas (for example, as found to occur in some desert oases by some authors [*e.g.* Biebach, 1990] but not by others [Salewski et al., 2010]). However, the poorer the physical state the higher may be the inclination to stop at the first available site, irrespective of its habitat suitability, or to put a limit to searching behaviour (*cf.* Yosef et al., 2006). For these birds, flying further in search of potentially better areas may be too risky or even impossible. A likely scenario in birds landing on the Balearics after sea-crossing.

In spite of being less suitable as a stopover site, the dry Balearics are often the first sites encountered by migrants and, correspondingly, act as attraction points for many birds (both of the wetlands studied here are located on the northern coast of two of the largest Balearics islands). The much higher capture indexes obtained in the dry Balearics compared to the wet Balearics testifies to this fact. On average capture indices are four times higher in dry than in wet sites, although, interestingly, this attraction effect not only occurs on somewhat isolated islands, but also on tiny islands that lie extremely close to the 'mainland' (a much larger island in this case). A typical case is that of L'Illa de l'Aire, a mere

Table 1. Differences (in %) in mean body mass between the four main study areas and the dry Balearics in birds trapped in spring. For samples and means, see Table 1 of the respective species accounts (differences are given only when at least five birds were measured in both areas).

Species	Wet Balearics	Els Columbrets	Catalonia	N Morocco
Streptopelia turtur	2.1	-2.7	-2.8	
Merops apiaster		20.3	2.6	-0.3
Upupa epops	-5.2	4.1	-4.9	
Riparia riparia	-5.7	7.9	-14.5	
Hirundo rustica	-7.9	9.3	-7.8	-15.5
Delichon urbicum	-11.7	7.6	-6.6	
Anthus trivialis	-6.3	5.0	-4.4	
Motacilla flava	-12.7	9.5	-7.0	
Erithacus rubecula	-6.8	4.9	-3.1	-12.2
Luscinia megarhynchos	-7.9	4.6	-2.8	-4.1
Phoenicurus phoenicurus	-7.5	3.4	-0.9	-5.0
Saxicola rubetra	-1.4	6.3	-0.6	-8.8
Turdus philomelos	-2.2	-2.4	-7.5	
Locustella naevia		-0.9	-7.2	-0.6
Acrocephalus schoenobaenus	-18.9	-4.2	-9.7	-5.0
Acrocephalus scirpaceus	-3.2	7.2	-3.6	2.4
Acrocephalus arundinaceus	-12.0	8.8	-5.6	-6.9
Hippolais icterina		9.7	-1.3	-10.7
Hippolais polyglotta		4.0	-4.2	-0.9
Sylvia cantillans	-2.7	2.3	-4.5	-11.0
Sylvia communis	-7.7	2.2	-3.4	-5.1
Sylvia borin	-8.3	4.9	-4.2	-7.4
Sylvia atricapilla	-3.2	2.3	0.4	-9.1
Phylloscopus bonelli		7.5	-1.7	-2.2
Phylloscopus sibilatrix	-5.7	10.0	-3.1	-7.5
Phylloscopus collybita	-6.3	1.4	-5.6	-7.8
Phylloscopus trochilus	-4.1	5.5	-0.7	-1.6
Muscicapa striata	-8.8	7.8	-5.5	-9.9
Ficedula hypoleuca	-6.1	8.1	-3.7	-6.0
Lanius senator	-14.7	8.1	3.1	3.3
Mean	-7.0	5.4	-4.0	-5.7
SD	4.5	4.8	3.6	4.8
n	25	30	30	23

1 km off the cost of Menorca. There, the mean daily number of captures is much greater than at S'Albufera d'Es Grau (13 times so in a forest species such as the Willow Warbler), a site which lies on Menorca just 17 km further north and with much better stopover options (as indicated by the results presented here and as would be expected in terms of habitat cover; *cf.* Kitirov et al., 2008). Moreover, as mentioned above, these small offshore islands not only attract birds in poor body condition. Therefore, these findings strongly suggest that in the Balearics the selection of stopover sites is often highly influenced by geographic and meteorological factors. Under this scenario, birds in a large range of physical conditions will end up landing at any given site, but poorer condition on average may lead to a greater probability of landing at the first available site, rather than to an increased inclination to search for a potentially better but more distant stopover site. Wetlands, moreover, are scarce in the Balearics and thus are often not just a short flight away.

The differences detailed here in average body mass between the wet and dry Balearics may also reflect differences in the refuelling options offered by both areas. Fuel deposition rates in wet Balearics tend to be more positive than in the dry Balearics and, accordingly, birds trapped there may include a higher proportion of birds that have already been at the site for a few days (or in the surrounding area) and that have recovered part of the energetic reserves lost during the long flight from N Africa. Moreover, at these sites, a greater proportion of dominant birds may also be present (e.g. males of some warblers that hold territories during migration; Cramp, 1992), which may also lead to an increase in the average condition and size of birds trapped there.

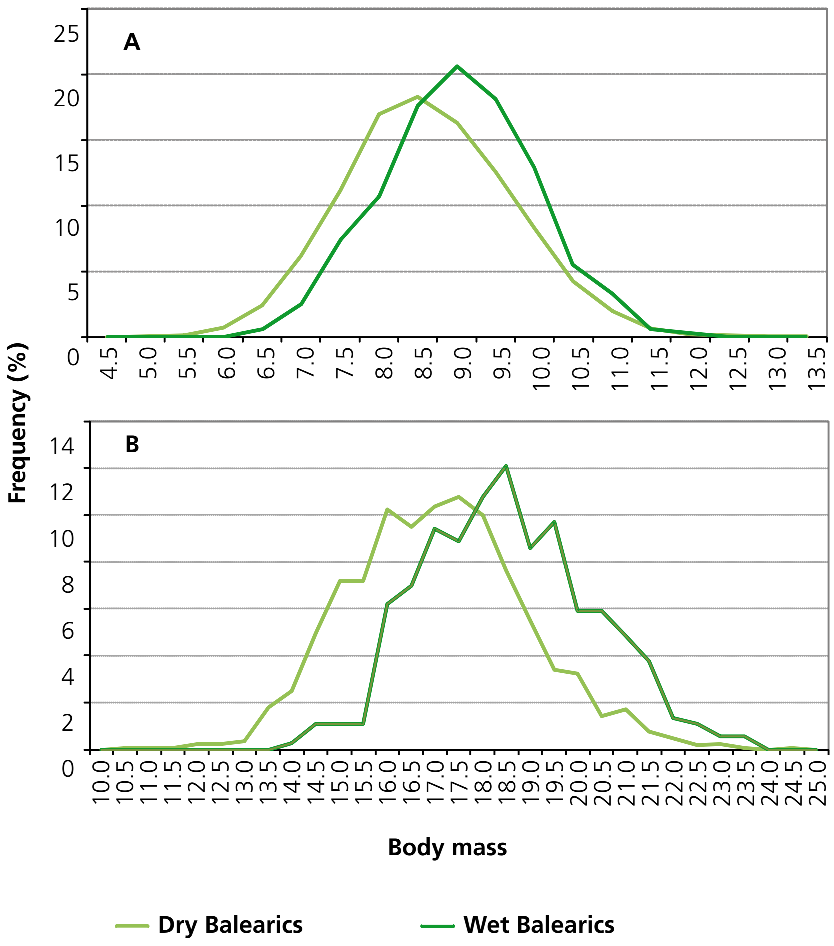

Figure 1. Frequency distribution of body mass in Willow Warbler (A) and Common Swallow (B) in the dry and wet Balearics.

Kerbacha *versus* Las Chafarinas

Differences between the dry and wet Balearics are in many ways paralleled by Las Chafarinas and Kerbacha. The islands of Las Chafarinas lie a mere 4 km off the north coast of Morocco and, in a contrast that resembles the differences between the dry and wet Balearics, are drier and much more sparsely vegetated than Kerbacha, a riverine site dominated by a tamarix forest. Out of 13 species for which enough data was available, in eight (62%) mean body mass was significantly lower in Las Chafarinas than in continental sites in N Morocco (above all Kerbacha). In the case of the Willow Warbler, birds from Las Chafarinas also had on average shorter third primaries. The interesting fact here is that Las Chafarinas lie to the north of the continent and so are not normally the first site that birds encounter during spring migration. It seems rather improbable that a higher proportion of birds in poorer physical condition ends up stopping in such a comparatively desolate area after overflying much better stopover sites just a few kilometres to the south. In fact, when confronted with an ecological barrier birds with lower fat reserves seem to be more likely to turn back in search of more suitable stopover sites rather than risk a sea-crossing (Bruderer & Liechti, 1998; Chernetsov, 2006).

In this case it would seem that the lower body mass and poorer condition of birds trapped on Las Chafarinas is a reflection of the relatively large number of birds that, having begun a sea-crossing, are forced to change or reverse flight direction due to unfavourable meteorological circumstances or energetic constraints. These birds would be expected to have on average lower fat reserves and body masses, because birds in poorer condition are likely to be more inclined to reverse movements and also because of the extra cost that a return flight supposes. Furthermore, the Willow Warblers trapped on these islands also had shorter average primaries since smaller or shorter-winged birds are more prone to suffer in unfavourable circumstances (*e.g.* particularly strong head winds; *cf.* Saino et al., 2010). Return movements from the sea in birds facing a large geographical barrier can represent 10–14% of all migrants (Bruderer & Liechti, 1998) and thus account also for a relevant proportion of the total birds trapped. In this case, Las Chafarinas would be the first available stopover site, which, together with the already well-known attraction effect, would mean that a higher proportion of these birds are trapped there than on nearby continental areas to the south.

Differences between continental and insular areas and between the islands of the W and C Mediterranean

Continent *versus* islands

The differences in body mass and refuelling options reported here between the dry and wet Balearics complicate the interpretation of the data from these islands. The two study sites in the wet Balearics are distinct because they are located on (1) large islands and (2) in wetlands, the latter a very scarce habitat in the Balearics. On the other hand, the data obtained in the dry Balearics comes from a much greater number of sites, some from small and somewhat isolated islands and islets, but others from sizeable islands such as Formentera. Moreover, although the range of habitats encountered in the dry Balearic sites are likewise not representative of the area as a whole, they are possibly more homologous - in terms of stopover suitability - to the Mediterranean forests, scrublands and dry arboreal croplands characteristic of most of the Balearics. All this suggests that the body mass of birds landing in most of the Balearics is closest to that reported herein from the dry Balearics sites. The fact that in many species average body mass in the wet Balearics was similar or even higher than in Catalonia would certainly seem to indicate that birds from this latter area represent a more exceptional subsample than those from the dry Balearics.

A comparison with data from N Africa also points in the same direction. Radar and infrared studies show that most birds take 5–8 hours to cross from N Africa to the southern coast of Mallorca (Bruderer, 2001), which, according to the average ground speed recorded in the area (48 km/s) and assuming a constant rate of mass loss of 1% (Delingat et al., 2008), implies a total mass loss of *c.* 5.5-9.1%. Since most birds migrating over the Balearics do not seem to stop before dawn (Liecthi et al., 1997), it could be assumed that many make non-stop flights of *c.* 9-10 hours, which would imply a somewhat greater reduction in mass of *c.* 10.4-11.7%. On average, body mass in the dry Balearics is *c.* 5.7% lower than in N Morocco (table 1). However, it should be taken into account that although the mean body mass recorded in these islands seems to be a good estimator of arrival mass (given the usually short stopover time and lack of mass gain recorded), the mean body mass recorded in N Morocco undoubtedly underestimates true departure body mass. Therefore, these considerations also suggest that data from the dry Balearics is more representative of the bulk of birds migrating through the Balearics in spring or, at least, to those stopping in the area. If most birds flying over the Balearics do not land there before dawn (see above), birds trapped on these islands will include a higher proportion of birds originating from further inland in N Africa than those passing through earlier during the night and, thus, have lower reserves (at the time they reach the islands) than those flying directly to continental Europe in long non-stop flights.

As a rule, mean body mass in the dry Balearics and Els Columbrets was lower than in Catalonia. Differences were significant in most species (27 out of 30), although in six cases only with respect to Els Columbrets. These differences certainly reflect the different refuelling conditions found in these two areas and the lower energetic demands made on birds flying over continental areas. As observed in many of the species studied here, birds migrating through continental Spain seem to move largely by means of short flight bouts and brief stopovers during which they usually gain some limited mass or at least maintain their fuel loads (in Catalonia positive significant fuel deposition rates were recorded in 10 species and negative rates in three out of 28 species analysed). However, birds passing through the Balearics and Els Columbrets are exposed to much more energetically demanding non-stop flights and, except those that take advantage of wetlands, have less opportunities to refuel successfully. Even in the dry Balearics, which offer better refuelling options than Els Columbrets, significant positive fuel deposition rates were only recorded in four species, while negative rates occurred in 11 cases (n = 29 species).

Differences between the Balearics and the Tyrrhenian islands

In most species, birds trapped in the dry Balearics tended to be in better condition than those from the Tyrrhenian islands. On average across species, in the dry Balearics body mass was 4.0% higher, although physical condition, which accounts for differences in size, was 5.9% better (table 2). These differences apparently reflect the different length of the stretches of open sea that birds have to cross to reach these areas (*c.* 230-320 km in the case of Balearics and *c.* 450-630 km in the Tyrrhenian islands). Moreover, birds migrating through these Italian islands also have to cross a longer, harsher part of the Saharan desert (Pilastro & Spina, 1997; Rubolini et al., 2002) and thus probably reach the north African coast more energetically stressed than their counterparts migrating further to the west.

The relevance of the distance from the north African coast is further underlined by the situation of Els Columbrets. This tiny archipelago is the most distant from N Africa (*c.* 375 km) of all our insular study sites and is also the most isolated. In 26 out of the 30 species studied, mean body mass was higher in the dry Balear-

Table 2. Comparison of mean body mass and physical condition between the Tyrrhenian islands and the dry Balearics in birds trapped in spring (differences shown as percentages). Values from the Tyrrhenian islands calculated from sample sizes and means given in Spina et al. (1993) and Pilastro & Spina (1997).

	Body mass			Physical condition		
Specie	Tyrrhenian islands	Dry Balearics	Difference (%)	Tyrrhenian islands	Dry Balearics	Difference (%)
Streptopelia turtur	122.6 (115)	128.8 (835)	5.1	0.691 (115)	0.743 (677)	7.5
Upupa epops	62.5 (246)	63.9 (447)	2.3	0.424 (246)	0.442 (378)	4.2
Hirundo rustica	16.7 (426)	17.1 (1740)	2.0	0.174 (426)	0.178 (1557)	2.3
Delichon urbicum	14.8 (134)	14.8 (228)	0.5	0.175 (134)	0.181 (192)	3.0
Anthus trivialis	18.0 (454)	20.7 (678)	15.0	0.265 (454)	0.309 (609)	16.5
Motacilla flava	13.9 (141)	15.9 (225)	14.0	0.226 (141)	0.263 (207)	16.4
Erithacus rubecula	14.5 (2390)	15.4 (6785)	6.2	0.269 (2390)	0.286 (6184)	6.0
Luscinia megarhynchos	19.2 (608)	19.5 (2122)	1.3	0.296 (608)	0.304 (1915)	2.8
Phoenicurus phoenicurus	13.2 (557)	14.1 (6309)	6.4	0.215 (557)	0.231 (5789)	7.3
Saxicola rubetra	14.4 (518)	16.0 (1940)	11.1	0.250 (518)	0.281 (1726)	12.5
Turdus philomelos	59.7 (355)	63.5 (394)	6.3	0.671 (355)	0.716 (379)	6.7
Locustella naevia	13.2 (23)	13.0 (297)	-1.6		0.266 (277)	
Acrocephalus schoenobaenus	10.7 (231)	10.6 (125)	-0.2	0.206 (231)	0.211 (118)	2.3
Acrocephalus scirpaceus	10.5 (44)	11.1 (733)	5.8	0.202 (44)	0.215 (664)	6.4
Acrocephalus arundinaceus	26.7 (61)	27.8 (74)	4.1	0.358 (61)	0.384 (59)	7.1
Hippolais icterina	12.0 (515)	12.6 (492)	5.7	0.195 (515)	0.207 (379)	6.1
Sylvia cantillans	9.2 (4011)	8.9 (2152)	-3.2	0.198 (4011)	0.195 (2036)	-1.4
Sylvia communis	13.3 (1431)	13.9 (6057)	4.4	0.239 (1431)	0.254 (5443)	6.5
Sylvia borin	15.7 (1627)	16.5 (5621)	4.9	0.255 (1627)	0.274 (5055)	7.4
Sylvia atricapilla	17.0 (896)	17.9 (4598)	5.3	0.307 (896)	0.318 (4381)	3.5
Phylloscopus bonelli	7.2 (28)	7.1 (738)	-0.8		0.148 (705)	
Phylloscopus sibilatrix	8.2 (1381)	8.9 (775)	9.0	0.139 (1381)	0.153 (646)	9.8
Phylloscopus collybita	7.0 (1010)	7.1 (3481)	1.4	0.159 (1010)	0.161 (3319)	1.4
Phylloscopus trochilus	8.2 (2475)	8.6 (28547)	5.9	0.160 (2475)	0.169 (26951)	5.6
Muscicapa striata	13.4 (355)	13.0 (3296)	-2.9	0.197 (355)	0.201 (2987)	2.0
Ficedula hypoleuca	10.8 (1172)	11.5 (4883)	5.9	0.176 (1172)	0.189 (4356)	7.4
Lanius senator	33.2 (336)	31.6 (1417)	-4.8	0.438 (336)	0.432 (1276)	-1.5
Mean			4.0			5.9
SD			4.8			4.5
n			27			25

ics than in Els Columbrets by on average c. 5.4% (table 1). A difference that is only slightly lower than that observed in comparison with the Tyrrhenian islands.

Crossing the W Mediterranean Sea in spring

Are birds more likely to cross over open sea in spring than in autumn?

In many species differences in the routes followed to cross the W Mediterranean Sea in autumn and spring are known to occur. In autumn movements in a south-westerly direction predominate in Europe and birds concentrate in C and W Iberia before they reach or overfly NW Africa; in spring, however, birds return along a more direct easterly (or central) route that leaves most of W Iberia devoid of birds, but increases the numbers passing through the Balearics (Alerstam, 1990; Cramp, 1992; Bruderer & Liechti, 1999; Telleria et al., 1999; Newton, 2008). We have observed this 'loop migration' pattern in 17 of the 28 species studied, in four cases further corroborated by recoveries. In the western Sahara birds also concentrate further westwards in autumn, but return on a broader and more direct front in spring (Trösch et al., 2005). In the only two species studied that largely move towards SE Europe in autumn, Icterine and Wood Warblers, a different but equivalent shift in their preferred routes has also been found, again in agreement with previous results (Zink, 1973; Cramp, 1992) and indicating that birds return in spring along a more westerly but more direct route than in autumn.

These differences in the main routes followed in autumn and spring indicate that a greater proportion of long-distance migrants passing through the W Mediterranean move directly across the sea in spring than in autumn. The large numbers of captures in spring on Mediterranean islands (Spina et al., 1993; Spina & Volponi, 2008, 2009; present work) provide a clear indication of this phenomenon; in addition, trans-Saharan migrants are comparatively less common in autumn than in spring in the Balearics (GOB, unpubl.). In fact, in the present work we have only detected a clear tendency to avoid passing through the Balearics in a few species, mostly those linked to wetlands (*e.g.* Reed and Great Reed Warblers), which may find it particularly difficult to find suitable stopover sites on these islands, and in the Melodious Warbler, a species known to circumvent the Mediterranean through continental Spain and S France (Pilastro et al., 1998). The situation is different in short-distance migrants, since many winter in NW Africa and therefore cross the Mediterranean in large numbers in both spring and autumn (Bruderer & Liechti, 1999; GOB, unpubl.).

The selection of a shorter, more direct route can also reduce the total duration of the migration and thus guarantee the earlier arrival on breeding grounds sought by many birds in spring (Alerstam, 1990; Newton, 2008). In fact, several sources indicate that migration in spring takes place at a faster rate than in autumn (Fransson, 1995; Newton, 2008). However, despite the need to shorten the route may also have played a role, loop migration patterns seem to have been largely modelled by seasonal differences in prevailing winds and other biogeographical factors (Newton, 2008).

Unusual movements and their links with meteorological conditions

In spite of these general differences found between autumn and spring migration routes, the exact routes followed by birds crossing the Mediterranean seem to be subject to a large degree of variability. A total of 18 recoveries of eight species detailed here (10 for Willow Warblers) suggest that marked differences exist from one year to another in the specific routes followed by individual birds. Most of the cases (14) refer to birds trapped in NE Spain and the Balearics in one spring and in Italy or Tunisia in another, which would indicate that birds cross the Mediterranean at longitudinally very distant sites in different years (up to *c.* 1,500 km apart). The meteorological conditions encountered by birds while attempting to cross the Mediterranean may explain such variability. Birds that have to face unfavourable weather conditions, above all storms and adverse winds, while flying over continental areas can always land; however, this is often impossible while crossing large expanses of open sea. In the event of strong head- or cross-winds, birds flying over the sea may prefer to be drifted longitudinally for large distances or even southwards rather than try to continue into the wind and risk running out of fuel whilst over the sea (Alerstam, 1990; Newton, 2008). Although to a lesser extent, this drift can also occur while crossing the Sahara since suitable stopover areas are much scarcer than in mainland NW Africa or Europe.

The effects of weather on birds crossing the Mediterranean are further exemplified by the reverse movements revealed by the recoveries of four species (Subalpine Warbler [3 birds], Spotted Flycatcher [2], Nightingale [1] and Melodious Warbler [1]). The majority of these recoveries seem to reflect return flights of migrants that had overshot their breeding sites. In most cases, in such movements taking place within the Balearics/Els Columbrets the distance flown back is relatively short (130-260 km), although in a few cases (Nightingale and Melodious Warbler) these distances can reach nearly 1,000 km. Six out of the seven birds showing this type of movement were first trapped to the east of their presumed breeding grounds, a further indication that birds were probably blown there by dominant westerly winds (*cf.* Barriocanal, 2007).

The number of reverse movements detailed here between the islands contrasts with the scarcity of recoveries in the opposite direction which, at first glance, would be expected to occur in greater number given the overall northward component in movements of spring migrants. In fact, we only report one case here, that of a Woodchat Shrike breeding on Menorca and captured on Cabrera 39 days beforehand. This all but total lack of northward recoveries within the Balearics/Els Columbrets reflects the fact that the vast majority of birds that continue northwards from these islands do so via long-distance flights that will take them directly to continental NE Spain or France (*cf.* Bruderer et al., 1996; Liechti et al., 1997).

Do birds migrating across the sea move in a more northerly direction than those crossing nearby continental areas?

In six out of 13 species with available data, recoveries from the Balearics/Els Columbrets seem to show more direct due northerly flight directions and less of an E European origin than in birds trapped in Catalonia. In some cases (*e.g.* Reed Warbler and even Blackcap) this pattern is fairly obvious and, despite the generally small sample sizes and some uncertainty on the real destination or origin of birds (see the Methodological introduction for more details), would seem to be genuine. Radar studies in the Balearics have also shown that birds crossing the Mediterranean Sea move in a more due northerly direction than in nearby European continental areas, *e.g.* S France, where NNE or NE movements are the rule (Bruderer et al., 1996; Speich, 1999). If birds cross the Mediterranean along a more direct due northerly direction instead of heading NNE or NE, they can substantially reduce the distance that they have to cover over open water (Bruderer et al., 1996) and thus reduce the risks inherent in such flights.

Above all in species such as the Reed Warbler, which seems to avoid long sea-crossings, the more due northerly average flight direction observed on the islands may

Table 3. Fuel deposition rate (as % of lean body mass per day) and minimum stop-over length in six species trapped in N Morocco in spring. Only species with significant refuelling rates are shown. Lean body mass calculated as average body mass of birds with a 0 fat score (all study areas). Means ± 95% confidence intervals and sample sizes are given.

Species	Fuel deposition rate	Minimum stop-over length	Lean body mass
Luscinia megarhynchos	1.67 ± 0.97 (39)	4.93 ± 1.22 (54)	17.80 ± 0.17 (614)
Acrocephalus schoenobaenus	2.54 ± 2.00 (5)	7.00 ± 3.51 (5)	9.41 ± 0.28 (46)
Acrocephalus scirpaceus	1.36 ± 0.57 (104)	5.89 ± 0.93 (143)	10.14 ± 0.09 (395)
Acrocephalus arundinaceus	2.54 ± 1.95 (6)	4.30 ± 1.46 (10)	27.49 ± 0.82 (67)
Sylvia borin	3.01 ± 2.20 (12)	2.31 ± 0.85 (26)	14.71 ± 0.09 (805)
Phylloscopus trochilus	2.60 ± 1.48 (34)	3.24 ± 0.76 (49)	8.12 ± 0.11 (226)

reflect the fact that a large number of birds crossing the Mediterranean are following a more direct route, perhaps because they have been delayed and need to make up time (*cf.* Barriocanal & Robson, 2006). The comparatively higher number of recoveries of birds apparently originating in the British Isles that pass through the Balearics/Els Columbrets (*e.g.* Blackcap, Sedge Warbler, Redstart) may also reflect a greater presence in these islands of birds undertaking more direct return movements.

Drifting is a final but probably rather significant factor that may also help to explain these differences in flight directions between insular and continental areas. As described above for birds making reverse movements, eastward rather than westward drift would seem to be the most common situation given the prevailing westerly winds in the W Mediterranean. Accordingly it would be expected that many more birds end up being captured in the Balearics/Els Columbrets after drifting from the west than from the east, both due to the prevailing winds and the fact that more birds pass to the west than to the east of these islands (the spring passage of birds between N Morocco and SE Spain may be more than three times greater than in the open sea east of the Balearics; Liechti et al., 1997; Bruderer & Liechti, 1999). Once these birds redetermine their migratory direction to compensate for wind displacement (*cf.* Moore, 1990), their subsequent movements may end up artificially increasing the northerly and even NNW component of recoveries from the islands.

The role of NW Africa during spring migration

In 10 out of the 11 species analysed in N Morocco fuel deposition rates were positive and in six cases significantly so (birds retrapped the day after first capture were excluded to avoid possible handling effects; Schaub & Jenni, 2000; Schwilch & Jenni, 2001). Of those species with significant refuelling rates, daily deposition represented 1.4-3.0% of lean body mass (mean 2.3%), which, taking into account average minimum stopover lengths, gives average mass gains of *c.* 10.1% of lean body mass (table 3).

Sample sizes of retraps were usually small and limited to a few species, however, the comparison of mean body mass in S and N Morocco indicates that mass gain in NW Africa is rather generalized in the studied species (table 4). Across species, the average body mass recorded in northern coastal areas of NW Africa (Morocco and Tunisia) were 12.2% higher than that obtained in SE Morocco (11.6% higher if data from Tunisia are excluded). However, as mentioned above, mean body mass recorded in N Morocco undoubtedly underestimates true departure body mass, particularly in birds that have to undertake long non-stop flights over the Mediterranean. In this respect, it should be noted that birds flying directly from N Africa to S France or NE Spain would require a minimum initial fuel load of *c.* 13%-18% (assuming a sea-crossing of *c.* 600 km, take-off areas up to 200 km inland from the N African coast, ground speed of 48 km/h and a constant rate of mass loss of 1%; Speich, 1999; Bruderer, 2001; Delingat et al., 2008).

As observed in the Balearics, body mass in different areas of SE Morocco may also vary according to habitat (or oasis size), although for the time being the pattern remains unclear and requires further study. In fact, some studies in the Sahara have found that mean body mass in migrants trapped in large oases is higher than in those captured in small ones or in very sparsely vegetated areas (Salewski et al., 2010), whilst others suggest the opposite (Biebach et al. 1986, Bairlein 1992). In Jorf and Figuig several species (*e.g.* Willow Warbler, Common Swallow) had higher mean body masses than in the much smaller oases of Defilia and Merzouga, although the possibility that this responds to inter-annual variations rather than habitat-specific conditions cannot be ruled out since datasets were collected in different years and sample sizes were somewhat limited. In fact, data collected at Jorf in 2005 (Maggini & Bairlein, 2011) show distinctly lower means than those reported here for 2006 at the same site and very similar figures to those from Defilia and Merzouga. On the other hand, in species such as Blackcap and Chiffchaff differences in body mass between different oases largely seem to reflect the fact that in these species the ratio of the number of wintering versus trans-Saharan migrants is higher in large oases. We consider, therefore, that in general terms the overall means detailed here for SE Morocco are rather

Table 4. Comparison of mean body mass between SE Morocco and N Morocco and N Tunisia in all species with available data from spring. Means and sample sizes (in brackets) are given. Values calculated using present data and all other available information for both areas (Ash, 1969; Smith, 1979; Cramp, 1992; Grattarola et al., 1999; Waldenström et al., 2004; Gargallo et al., unpubl.; see species accounts for further details).

Species	SE Morocco	N Morocco & N Tunisia	Difference (%)
Merops apiaster	51.4 (66)	55.8 (16)	8.5
Riparia riparia	11.3 (269)	13.3 (9)	17.8
Hirundo rustica	16.3 (2661)	19.0 (247)	16.8
Delichon urbicum	14.6 (281)	17.3 (6)	18.7
Anthus trivialis	18.5 (70)	23.5 (10)	26.8
Luscinia megarhynchos	19.4 (688)	20.5 (369)	5.7
Phoenicurus phoenicurus	13.0 (244)	14.9 (73)	14.7
Saxicola rubetra	14.0 (39)	17.1 (10)	22.5
Locustella naevia	11.7 (19)	13.1 (13)	11.8
Acrocephalus schoenobaenus	9.9 (161)	10.8 (144)	9.4
Acrocephalus scirpaceus	10.2 (414)	10.8 (1214)	6.4
Acrocephalus arundinaceus	27.1 (24)	29.7 (93)	9.6
Hippolais icterina	11.4 (9)	13.6 (31)	19.7
Hippolais polyglotta	10.2 (51)	10.7 (191)	4.1
Sylvia cantillans	9.0 (406)	9.8 (158)	9.0
Sylvia communis	13.8 (124)	15.3 (106)	10.5
Sylvia borin	17.1 (167)	18.0 (698)	5.5
Sylvia atricapilla	14.3 (246)	19.5 (361)	36.3
Phylloscopus bonelli	7.2 (244)	7.3 (11)	1.5
Phylloscopus sibilatrix	8.6 (84)	9.5 (101)	10.4
Phylloscopus collybita	7.0 (138)	7.5 (127)	6.1
Phylloscopus trochilus	8.2 (633)	8.7 (702)	6.8
Muscicapa striata	13.2 (37)	14.4 (66)	9.0
Ficedula hypoleuca	11.8 (249)	12.2 (179)	3.4
Lanius senator	28.1 (212)	32.4 (35)	15.2
Mean			12.2
SD			8.08
n			25

Table 5. Comparison between maximum body mass recorded in the Sahel in spring and mean body mass of birds trapped in SE Morocco. Means and sample sizes (in brackets) are given for SE Morocco (Ash, 1969; Gargallo et al., unpubl.; present data).

Species	Sahel	SE Morocco	Difference (%)	Reference
Anthus trivialis	36.5	18.5 (70)	-49.2	Smith (1966)
Motacilla flava	26.0	15.1 (297)	-41.9	Wood (1992)
Saxicola rubetra	26.0	14.0 (39)	-46.2	Smith (1966)
Locustella naevia	20.0	11.7 (19)	-41.5	Bayly et al. (in prep)
Acrocephalus schoenobaenus	19.5	9.9 (161)	-49.3	Fry et al. (1970)
Sylvia cantillans	16.5	9.0 (406)	-45.6	Ottoson et al. (2001)
Sylvia communis	29.5	13.8 (124)	-53.1	Ottoson et al. (2001)
Sylvia borin	32.5	17.1 (167)	-47.4	Smith (1966)
Sylvia atricapilla	30.0	14.3 (246)	-52.2	Ottoson et al. (2001)
Muscicapa striata	22.5	13.2 (37)	-41.3	Smith (1966)
Ficedula hypoleuca	22.0	11.8 (249)	-46.2	Smith (1966)
Mean			-46.7	
SD			4.1	
n			11	

representative of the bulk of the birds arriving in the area in spring. In any case, since data from N Morocco certainly underestimates real mean take-off mass of the area, the differences in body mass given here between S and N Morocco are probably fairly conservative.

Data from SE Morocco comes from sites located *c.* 1,500 km north of the Sahel. Following the approach of Salewski et al. (2010), and taking into account the average ground speed recorded in spring migrants in the Sahara (59 km/h) and a constant rate of mass loss of 1% (Delingat et al., 2008), birds covering this distance would lose *c.* 22% of their total take-off body mass if they used a non-stop migration strategy; but they would lose *c.* 33% in the more likely case (*cf.* Schmaljohann et al., 2007a, 2007b) that they undertake an intermittent strategy without refuelling en route. On average, mean body mass in 11 species captured in SE Morocco is 47% lower than the highest values recorded in the Sahel in spring (table 5), suggesting that an average total mass loss of *c.* 30-40% could be rather realistic. This figure indicates that, averaging across species, refuelling in NW Africa re-establishes approximately a minimum of *c.* 18-28% of the energetic reserves lost after crossing the Sahara, a gain that can be particularly relevant in birds that still have to cross the Mediterranean on a long non-stop flight.

This finding agrees with the suggestion that after winter rains NW Africa plays a relevant refuelling role for many birds (Moreau, 1961; Alerstam, 1990; Wood, 1992). In this respect, radar studies also have shown that the vast majority of birds migrating through the Mediterranean rest in coastal and adjacent inland areas of NW Africa (up to *c.* 250 km inland) and that, at least in passerines, the number of birds that fly non-stop across both the Sahara and the Mediterranean Sea is statistically irrelevant (Bruderer & Lieachti, 1999; Speich, 1999; Bruderer, 2001). The relevance of NW Africa in spring is also further corroborated by the fact that in many of the species studied here migrants (and often also recoveries) are more common in NW Africa in spring than in autumn (Zink, 1973; Alerstam, 1990; Cramp, 1992; present results).

Some studies based on birds trapped in the Tyrrhenian islands (Pilastro & Spina, 1997) have been interpreted as indirect evidence of a lack of substantial fattening up in NW Africa (Grattarola et al., 1999). However, the existence of refuelling in NW Africa and the key finding of these analyses, *i.e.* that the distribution of preferred habitats just south of the Sahara is the main factor constraining spring migration, are not necessarily contradictory.