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Body condition of migrant passerines crossing a small ecological barrier

By Volker Dierschke and Fabian Bindrich

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During migration, many passerine birds cross the southeastern North Sea (German Bight), an only small ecological barrier (< 150 km flight when migrating along southwest-northeast axis). In contrast to crossings of large barriers (e.g. Sahara desert, Mediterranean Sea), passerines stopping over on the small offshore island Helgoland in the German Bight carried only small or moderate fat reserves according to trapping results. In order to find out about a possible existance of a heavier fraction of migrants, which usually passes the island without stopovers, migrants were mist-netted early morning during departure. At the mist-netting site, passerines alighted during the night or at dawn move through the bushes and leave the island. No general difference was found in body condition (body mass, fat reserves) between birds caught early in the morning and those trapped later during the day. As adverse weather conditions might lead all birds aloft to ground on the island, we also looked at trapping data from big fall days (birds caught with three large funnel traps). However, big falls usually occurred with favourable conditions (except for complete cloud cover) and only in autumn a trend was found in several species that individuals trapped during big falls are slightly heavier than those trapped during the rest of the season. In another approach, weather during capture of the heaviest/fattest fraction of birds trapped was compared to conditions during capture of birds in average body mass and fat score, respectively. Only in autumn a tendency was found that strong headwinds and much overcast lead to captures and thus to stopovers of birds in body condition above average. Thus, no general difference between migrating birds and those stopping over is expected, verifying that fat reserves are kept low during the crossing of a small ecological barrier. In addition, body condition does not explain the decision to alight on a small island during such a short-distance migratory flight.

Key words: passerines, migration, body condition, ecological barrier.

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1. Introduction

During migration between breeding and non-breeding areas, most landbirds breeding in Europe face ecological barriers, areas where feeding or even resting is impossible. Large barriers such as the Sahara desert or the Mediterranean Sea require adaptations in premigratory and migratory behaviour, i.e. deposition of energy reserves sufficient to cover the flight distance (BAIRLEIN 1987, 1988, PILASTRO & SPINA 1997, YOM-TOV & BEN-SHAHAR 1995) or flight tactics regarding altitude and daytime to avoid dehydration (IZHAKI & MAITAV 1998, KLAASSEN & BIEBACH 2000). Smaller barriers are sometimes left aside by flying detours as observed in the Alps (BRUDERER & JENNI 1988) and over the North Sea (DROST & BOCK 1931, JELLMANN 1988). However, many birds take the direct way and cross the German Bight, the southeastern part of the North Sea, where migratory directions observed in the field and by radar are along a northeast-southwest as well as a north-south axis (DROST & BOCK 1931, JELLMANN 1977, BUURMA 1987). Therefore, landbirds have to cross c. 50 – 150 km or in the most extreme case c. 500 km (Norway-Germany) of unsuitable environment. Compared to several thousand kilometers to cover when crossing the Sahara (and possibly also the Mediterranean Sea without replenishing reserves in between, SPINA & PILASTRO 1999) much less fuel would be necessary to conduct a successful flight. Because extra fuel loads are costly regarding transport effort (KLAASSEN & LINDSTRÖM 1996) and predation risk (LIMA 1986, KULLBERG et al. 1996, LIND et al. 1999), energy reserves are expected to be much lower in the German Bight than in case of large barriers.

Although ecological barriers in general are adverse to foraging and even resting, some exceptions are available in the form of oases in the desert or islands in the sea. Passerine birds stopping over in oases often just wait for the next night in order to continue migration, whereas weak birds unable to cover the remaining stretch of the barrier crossing recover by foraging and refuelling (Bairlein 1985, 1987, Biebach 1985, 1995, Biebach et al. 1986, Lavee & Safriel 1989). The small ecological barrier German Bight also presents a stopover possibility, the small offshore island of Helgoland. For long time this island is well known for large concentrations of passerine migrants during both spring and autumn migration periods (Gätke 1900). As the mainland coast is only c. 50 km (i.e. 1 – 2 hours of flight for passerines) apart, it would be expected that only weak birds unable to reach the coastline take the opportunity to land on the island for a stopover. On the other hand, during adverse weather conditions even birds in good body condition would benefit from alighting in order to avoid danger or exhaustion.

In order to investigate the question, whether internal factors (body condition, migration strategy) or external factors (weather conditions) rule the decision about a stopover during a migratory flight in case of a small ecological barrier, we studied the migratory behaviour and body condition of passerines on the island of Helgoland. Because on Helgoland it is impossible to catch birds during active migratory flight at night, our aproach was to mist-net birds early in the morning which were about to take-off after grounding in the night or during the first daylight. At the study site, passerines typically move through the bushes and depart from the island early in the morning. If migrating birds (to be correct: birds not deciding to stopover during the day and thus leaving the island) were in better condition than resting birds, then the early morning departing birds would be expected to be heavier and to carry more fat reserves than birds trapped during the rest of the day.

Another approach to test for differences in body condition between migrating birds and those stopping over is to look at data of birds trapped following big falls of migrants. Suggesting such falls occur when extreme weather situations force many birds to alight on the island, then those birds should be in better condition compared to birds captured on days with weather conditions allowing birds to continue migration without stopping over on Helgoland. The other way round, this hypothesis would imply that birds in good condition are trapped particularly during adverse weather conditions. Such a pattern of body condition at arrival was observed after the long flights across the Gulf of Mexico (Moore & Kerlinger 1987) and is in line with higher body mass levels during foggy nights in migrating passerines trapped at an Alpine pass (Bruderer & Jenni 1988). We therefore compared weather conditions in the morning before trapping among groups of birds in different body condition. Finally, in two cases it was possible to compare body condition of passerines killed at towers during nocturnal flight with those trapped early in the next morning and/or during the next day.

2. Methods

The island of Helgoland is situated in the southeastern North Sea (German Bight; 54° 11' N, 07° 55' E) in a distance of 43 km to the Wadden Sea island Wangerooge to the south and 53 km to the mainland coast both to the east and south. Due to the small size (1.5 km^2) and the dominance of open habitats (grassland, beach, dunes, village), many migrant birds concentrate in the few available groups of bushes and small trees. Passerine migrants were trapped in two different situations.

In the trapping garden, cultivated with bushes and trees and run since 1910, birds were captured in three large funnel traps seven times each day between 08.30 and 17.30 hours local time (for details see Moritz 1982). This study refers to the years 1990 – 1999, when most birds were measured (length of primary 8 to the nearest 0.1 mm, Jenni & Winkler 1989) and weighed (to the nearest 0.1 g with an electronic balance). From 1995 – 1999 (thrushes: autumn 1996 – 1999), visible fat reserves were estimated on a nine class scale (Kaiser 1993).

The other study site on Helgoland was the Mittelland, a big crater emerged from a big blasting in 1947 and now having slopes grown by bushes. Mist-netting there took place in the periods 9 April – 3 June 1998 (nets open during 65 hours on 26 days), 10 August – 9 October 1998 (85 h on 30 days), 16 April – 4 June 1999 (77 h on 36 days) and 10 August – 15 October 1999 (129 h on 54 days). Up to seven mist-nets (6 m long with four shelves) were set in four places between dense bushes. The number of nets varied due to weather conditions (wind, rain). Nets were controlled every 15 – 30 minutes and extracted birds were measured in the same way as in the trapping garden. As an index for the abundance of migrants we calculated the birds trapped per net hour. Retraps were not considered in this study except for calculating a retrap rate. On 1 May 1998, 28 Willow Warblers accidently killed at the lighthouse were collected and measured several hours later. On 16 October 2000, the same was done with 77 Song Thrushes which were killed at a telecommunication tower, but measurements were taken after stored deep-frozen.

Body mass measured (BM_m) was corrected for body size (length of primary 8, P8) as standardized body mass (BM_s) by

$$BM_{s,i} = BM_{m,i} + x\ (P8_{mean} - P8_i)$$

with x as the ascent in the linear regression of body mass against P8 for all individuals with fat score 2 (calculated for spring and autumn migration separately).

In order to examine diurnal variation of body condition, trapped birds were grouped into those mist-netted until 2 h after sunrise, mist-netted 2–5 h after sunrise, caught in funnel traps a.m. (08.30 – 11.30 hours) and p.m. (15.30 – 17.30 hours). The time of sunrise changed from 06.39 hours (9 April) to 04.58 hours (4 June) and from 05.54 hours (10 August) to 07.53 hours (15 october). Comparisons were made between the early and late captures within mist-netted birds (fat scores, body mass) and within those caught in funnel traps (body mass), respectively, and between the total of mist-netted birds and those from funnel traps before noon (body mass). Differences were tested for significance with Mann-Whitney-U-test (fat scores) and one-way ANOVA (body mass).

According to our hypothesis, the fraction of birds with high fat loads should only alight on the island when weather conditions for migration deteriorate and make it unfavourable to continue migration. As this should not affect single birds but all birds aloft, in a first step days with big falls of single species were tested for weather conditions which might have been responsible for the fall. For both seasons (spring and autumn migration) separately, days exceeding 1.5 % of the ten-year-total (1990 – 1999) captured in the funnel traps were selected for several species. For these days and for those with more than 200 birds trapped of all species, weather data of 07.30 hours local time obtained from Deutscher Wetterdienst, Wetterstation Helgoland, were examined (precipitation, wind, visibility, cloud cover). Wind was referred to as the tailwind component TWC = cos (v) x wind speed [m s^{-1}] with v as the deviation of the observed wind from tail wind for migrating birds (FRANSSON 1998). According to recoveries of birds ringed at Helgoland (ZINK 1973 – 1985), the major migratory direction is along a SW-NE-axis. Therefore, tail wind was considered to be from SW in spring and from NE in autumn. Negative TWC values were treated as headwinds and those positive as tailwinds. Average body mass of birds captured during big falls was compared with all the other birds of the same species in the same migratory season and year (tests for significant differences with one-way ANOVA).

In another approach to examine the relation between weather and body condition of birds alighted on Helgoland, average wind conditions (TWC) and cloud cover in the morning (07.30 hours) before capture of each individual in the funnel traps were calculated for three groups of body mass and three groups of fat content, respectively. When ranked for body mass, the individuals of a species captured were grouped into light birds (the 10 % lightest individuals), intermediate birds (the median 50 % of individuals) and heavy birds (the 10 % heaviest individuals). Fat content groups consist of lean birds (fat scores 0 – 1), intermediate birds (fat scores 2 – 3 in most species, but 2 – 4 in Garden Warbler* and Blackcap) and fat birds (4 – 5 in most species, but 5 – 7 in Garden Warbler and Blackcap). The difference in grouping is due to the different occurrence of fat scores in the species examined (cf. Table 2).

During ringing operations in the Mittelland in spring and autumn 1999, the number of passerines migrating, arriving and departing was observed daily and summarized according to a seven-category scale (Table 1), in which especially the timing of arrivals and departures were considered. Usually the categories with higher numbers coincided with more birds around, but this was difficult to measure. The daily pattern of migration was compared to the results of mist-netting.

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* For scientific names see Table 2.

3. Results

3 1 Characterization of passerine migration

In 1999, observations of the pattern of passerine migration during spring and autumn migration periods showed no or weak visible migration on the majority of days (categories 1 – 3 in Table 1). Strong migration with many birds on the ground as well happened only on a few days, but in autumn produced the best trapping results, especially when birds were alighting and departing both at night and in the morning (categories 4 – 7 in Table 1). During mist-netting, retrap rates were low in spring (17 retraps, i.e. 3.3 % of ringed birds) as well as in autumn (29 retraps, i.e. 2.0 %). The only few birds mist-netted in the Mittelland and recaptured 600 m further north in the trapping garden (5 birds, i.e. 1.0 % in spring and 12 birds, i.e. 0.8 % in autumn) further demonstrate a low proportion of birds staying instead of leaving the island.

Table 1: Observed migration patterns of passerines in and around the Mittelland (Helgoland) and the related mist-netting results during spring and autumn migration 1999. Categories refer to the occurrence (+) of arrivals at night (bird activity in the bushes already before sunrise) and in early morning (until 2 h after sunrise) as well as to departures in early morning and late morning (2 – 5 h after sunrise).

Tab. 1: Charakterisierung des Vogelzuges im und um das Mittelland auf Helgoland in Beziehung zu den Ergebnissen des dortigen Japannetzfanges im Frühjahr und Herbst 1999. Die Kategorien beziehen sich auf das Vorkommen (+) des Einfalls von Singvögeln in der Nacht (Vogelaktivität in den Büschen schon vor Sonnenaufgang) und am frühen Morgen (bis 2 h nach Sonnenaufgang) sowie den sichtbaren Abzug von Vögeln am frühen Morgen und am Vormittag (2 – 5 h nach Sonnenaufgang).

category	arrivals		departures		spring migration		autumn migration	
	night	early morning	early morning	late morning	no. days	birds trapped per net hour	no. days	birds trapped per net hour
1					21 (50%)	0.21	15 (29%)	0.25
2	+				3 (7%)	0.80	6 (11%)	0.58
3		+			7 (17%)	0.53	5 (10%)	0.36
4	+	+	+		4 (9%)	1.14	18 (35%)	1.09
5		+	+		3 (7%)	0.41	3 (6%)	0.34
6		+	+	+	4 (9%)	0.82	3 (6%)	0.96
7	+	+	+	+			2 (4%)	5.09

3.2. Visible fat reserves in birds stopping over

Most passerine birds captured in the funnel traps showed low levels of visible fat reserves (Table 2). The great majority of birds was scored with 1 – 4, but large amounts of fat (scores 5 – 6) occurred in a small percentage of sylviid warblers. Birds with completely depleted fat reserves (score 0) also occur in a very low quantity (Table 2).

3.3. Diurnal pattern of fat scores

Fat scores taken during mist-netting in the Mittelland usually did not differ significantly between catches early in the morning and between 2 – 5 hours after sunrise in both spring and autumn (Table 3). The only exception refers to Robins in autumn, in which individuals were significantly fatter when trapped early. However, in some species weak individuals (fat score 0 – 1) predominated in the late morning catches in autumn (Reed Warbler, Chiffchaff, Robin, Song Thrush), but without producing significant differences in the average fat scores (Table 3). Thus, no general difference was observed in fat reserves between birds departing early in the morning and those resting during the day.

Table 2: Visible fat reserves (fat scores according to Kaiser 1993) of passerine birds captured in the funnel traps of the trapping garden on Helgoland from 1995 – 1999 (in species marked with * only from autumn migration 1996 onwards).

Tab. 2: Sichtbare Fettreserven (Fettstufen nach Kaiser 1993) von Singvögeln, die von 1995 – 1999 im Helgoländer Fanggarten mit Trichterreusen gefangen wurden (* Daten erst ab Wegzug 1996).

species			fat score (% of total)								
			0	1	2	3	4	5	6	7	mean
Wren *	spring	76		10.5	43.4	36.8	9.2				2.4
Troglodytes troglodytes	autumn	132	1.5	19.7	34.1	30.3	14.4				2.4
Dunnock *	spring	396	2.5	30.1	43.9	21.2	1.8	0.5			1.9
Prunella modularis	autumn	340	11.8	37.6	32.9	14.1	3.5	-	-	-	1.6
Robin *	spring	960	0.8	17.0	37.9	39.5	4.3	0.5			2.3
Erithacus rubecula	autumn	1514	5.5	30.0	39.4	21.4	3.6	0.1			1.9
Redstart	spring	696	0.1	5.0	30.6	52.9	10.3	1.0			2.7
Phoenicurus phoenicurus	autumn	1021	1.0	14.4	32.5	42.2	9.0	0.9			2.5
Blackbird *	spring	3745	1.1	33.5	46.5	18.0	0.9	0.1			1.8
Turdus merula	autumn	3328	0.7	15.1	42.0	35.4	6.7	0.1			2.3
Song Thrush *	spring	2374	1.4	33.2	43.9	19.9	1.6				1.9
Turdus philomelos	autumn	4325	3.9	41.3	39.8	14.3	0.7				1.7
Redwing *	spring	174	10.9	54.0	26.4	8.0	0.6				1.3
Turdus iliacus	autumn	1304	6.4	47.6	23.3	20.3	2.2	0.1	-	-	1.6
Reed Warbler	spring	112	10.7	19.6	42.0	20.5	6.3	0.9			1.9
Acrocephalus scirpaceus	autumn	78		10.3	14.1	21.8	19.2	23.1	10.3	1.3	3.7
Whitethroat	spring	250	0.8	7.2	27.2	43.2	18.0	3.2	0.4		2.8
Sylvia communis	autumn	200	0.5	4.0	10.0	31.0	29.0	22.0	3.5		3.6
Garden Warbler	spring	873	2.5	7.7	33.4	37.0	13.6	4.6	1.1		2.7
Sylvia borin	autumn	1310	2.3	20.5	36.9	25.2	8.9	4.7	1.5		2.4
Blackcap	spring	343	2.3	16.6	28.9	34.4	13.1	4.7			2.5
Sylvia atricapilla	autumn	1445	0.4	8.8	26.6	36.5	21.7	5.3	0.6		2.9
Chiffchaff	spring	421	2.6	21.4	42.5	30.6	2.9				2.1
Phylloscopus collybita	autumn	117	0.9	23.9	33.3	28.2	12.8	0.9			2.3
Willow Warbler	spring	498	0.8	5.4	16.3	48.0	27.1	2.2	0.2		3.0
Phylloscopus trochilus	autumn	889	0.7	10.6	29.9	48.9	9.1	0.8			2.6
Spotted Flycatcher	spring	239	2.9	26.4	49.4	21.3					1.9
Muscicapa striata	autumn	73	2.7	30.1	32.9	28.8	4.1	1.4			2.1
Pied Flycatcher	spring	128	1.6	10.9	32.0	44.5	9.4	1.6			2.5
Ficedula hypoleuca	autumn	616	1.9	18.5	39.1	33.8	6.3	0.3			2.3
Chaffinch *	spring	137	0.7	32.1	29.2	33.6	4.4				2.1
Fringilla coelebs	autumn	505	5.1	37.6	33.3	17.0	6.9				1.8

3.4. Diurnal pattern of body mass

When comparing mist-netted birds captured during the first two hours after sunrise and those trapped in the three subsequent hours, the only significant differences occurred in autumn Redstart, Willow Warbler, Garden Warbler (earlier birds lighter than later ones) and Song Thrush (earlier birds heavier than later ones; Table 4). Birds trapped in funnel traps showed little diurnal variation as well, but individuals captured a.m. were significantly heavier in spring and autumn Song Thrushes, and significantly lighter in spring Chiffchaffs and autumn Willow Warblers (Table 4). In autumn, between the two trapping sites differences between all birds mist-netted until 5 h after sunrise and

Table 3: Fat scores of passerines mist-netted in the Mittelland in early morning (until 2 h after sunrise) and late morning (2 – 5 h after sunrise). The P-values refer to the differences in mean fat scores between early and late trapped birds (Mann-Whitney-U-test).

Tab. 3: Fettstufen von Singvögeln, die im Mittelland am frühen Morgen (bis 2 h nach Sonnenaufgang) und am Vormittag (2 – 5 h nach Sonnenaufgang) in Japannetzen gefangen wurden. P-Werte beziehen sich auf Unterschiede in den mittleren Fettstufen zwischen den früh und spät gefangenen Vögeln (Mann-Whitney-U-Test).

species	early or late		fat score							mean	P
			0	1	2	3	4	5	6		
spring migration											
Redstart	early	22		18%	50%	27%	5%			2.2	
	late	7		14%	43%	43%				2.3	0.702
Whitethroat	early	17		6%	35%	29%	29%			2.8	
	late	7			29%	57%	14%			2.9	0.949
Garden Warbler	early	22			45%	14%	27%	14%		3.1	
	late	9			67%	22%	11%			2.4	0.192
Chiffchaff	early	82	1%	30%	37%	14%	16%	2%		2.2	
	late	30		27%	37%	30%	3%	3%		2.2	0.853
Willow Warbler	early	94		11%	29%	18%	29%	13%	1%	3.1	
	late	57		5%	32%	26%	26%	11%		2.8	0.937
autumn migration											
Robin	early	129	2%	29%	46%	16%	6%			1.9	
	late	70	3%	60%	19%	16%	3%			1.6	0.002
Redstart	early	56	5%	36%	25%	27%	7%			1.9	
	late	31		23%	58%	16%	3%			2.0	0.726
Song Thrush	early	38		24%	50%	18%	8%			2.1	
	late	15	7%	47%	33%	7%	7%			1.6	0.066
Reed Warbler	early	29			7%	17%	31%	34%	10%	4.2	
	late	15		7%	7%	27%	27%	33%		3.7	0.240
Garden Warbler	early	75	6%	15%	29%	35%	7%	8%		2.2	
	late	74	1%	12%	31%	32%	15%	4%	4%	2.8	0.197
Chiffchaff	early	29		14%	45%	28%	14%			2.4	
	late	13		31%	38%	31%				2.0	0.231
Willow Warbler	early	161	1%	9%	21%	22%	39%	8%		3.1	
	late	92		4%	16%	28%	43%	8%		3.4	0.269
Pied Flycatcher	early	84	2%	15%	26%	43%	13%			2.5	
	late	66		15%	27%	38%	18%	2%		2.6	0.491

those captured in funnel traps were significant in Robins (birds lighter in funnel traps), Redstarts, Garden Warblers and Blackcaps (birds lighter in mist-nets, Table 4). In most cases, statistically significant differences appear to be biologically small.

3.5. Body mass and weather conditions during big falls

Tested species by species, unusual high numbers of passerine birds trapped in the trapping garden did not coincide with weather unfavourable for migratory flights. In most cases, big falls of single species occurred with few precipitation, during tailwind conditions (which in the majority of cases improved during the night), and with good visibility (Table 5). This pattern is less clear in autumn

Table 4: Standardized body mass (mean ± sd) of birds captured in the Mittelland with mist nets and in the trapping garden with funnel traps. P-values refer to differences between early and late captures within one trapping site (one-way ANOVA). Differences between birds from mist nets (all birds) and from funnel traps (a.m. only) were significant in autumn for Robin ($P < 0.001$, one-way ANOVA), Redstart ($P < 0.001$), Garden Warbler ($P = 0.002$) and Blackcap ($P = 0.013$).

Tab. 4: Standardisierte Körpermasse (Mittelwert ± Standardabweichung) von Japannetzfängen aus dem Mittelland und Reusenfängen aus dem Fanggarten. P-Werte beziehen sich auf Unterschiede zwischen früh und spät gefangenen Vögeln innerhalb einer Fangstation (einfaktorielle ANOVA). Signifikante Unterschiede zwischen Vögeln aus Japannetzfängen (alle Vögel) und denen aus Reusenfängen (nur vormittags) gab es im Herbst bei Rotkehlchen (P < 0,001, einfaktorielle ANOVA), Gartenrotschwanz (P < 0,001), Gartengrasmücke (P = 0,002) und Mönchsgrasmücke (P = 0,013).

species	period	mist-netting 0 – 2 h after sunrise n	BM_S	mist-netting 2 – 5 h after sunrise n	BM_S	P	funnel-trapping 08.30 – 11.30 hours n	BM_S	funnel-trapping 15.30 – 17.30 hours n	BM_S	P
Robin	spring						676	16.91 ± 1.30	527	17.06 ± 1.30	0.061
	autumn	129	15.87 ± 1.27	71	18.80 ± 1.01	0.676	910	16.25 ± 1.21	732	16.27 ± 1.30	0.755
Redstart	spring						476	15.59 ± 1.10	214	15.71 ± 1.17	0.199
	autumn	56	13.89 ± 1.37	31	14.68 ± 1.10	0.008	653	15.17 ± 1.29	370	15.20 ± 1.26	0.681
Song Thrush	spring						2616	69.62 ± 5.37	960	68.88 ± 5.35	<0.001
	autumn	38	69.09 ± 4.88	16	65.33 ± 5.95	0.019	3776	69.12 ± 5.76	1899	68.51 ± 5.68	<0.001
Reed Warbler	spring						82	11.92 ± 0.93	28	12.03 ± 1.01	0.598
	autumn	29	12.60 ± 1.50	18	12.34 ± 1.50	0.611	50	12.43 ± 1.25	23	12.31 ± 1.46	0.711
White-throat	spring						184	15.19 ± 1.21	64	15.18 ± 1.35	0.960
	autumn						132	16.59 ± 1.62	63	16.71 ± 1.63	0.622
Garden Warbler	spring	22	18.55 ± 1.88	9	18.41 ± 1.12	0.837	577	18.44 ± 1.52	295	18.41 ± 1.58	0.783
	autumn	75	18.41 ± 1.86	73	19.21 ± 1.79	0.009	767	19.39 ± 2.18	561	19.47 ± 2.25	0.486
Blackcap	spring						242	18.15 ± 1.86	99	18.11 ± 1.42	0.844
	autumn	44	19.52 ± 2.80	5	19.18 ± 1.79	0.792	939	20.20 ± 2.11	508	20.19 ± 2.19	0.960
Chiffchaff	spring	82	7.47 ± 0.59	30	7.57 ± 0.56	0.442	259	7.49 ± 0.65	128	7.71 ± 0.63	0.001
	autumn	29	7.36 ± 0.57	13	7.10 ± 0.61	0.182	66	7.42 ± 0.60	42	7.52 ± 0.76	0.465
Willow Warbler	spring	94	8.99 ± 0.93	61	9.07 ± 0.78	0.564	321	9.03 ± 0.78	179	9.14 ± 0.79	0.110
	autumn	161	8.55 ± 0.96	92	9.00 ± 0.72	<0.001	427	8.71 ± 0.77	469	8.82 ± 0.74	0.023
Pied Flycatcher	spring						88	13.31 ± 1.15	45	13.68 ± 1.29	0.090
	autumn	84	12.31 ± 1.17	66	12.57 ± 1.11	0.169	349	12.78 ± 1.06	268	12.84 ± 1.12	0.526

migration, when some falls occurred with rainfall of more than 5 mm in the preceeding night, and half of the falls happened in deteriorating wind conditions. The great majority of fall incidents was recorded with complete or nearly complete cloud cover in autumn, but not so in spring (Table 5). These general results hold true for days with more than 200 birds trapped as well (Table 5).

During spring migration, body mass of trapped birds did not differ between big fall days and the other days of the same season in most cases (Table 5). In contrast, in many cases autumn migrants trapped during big falls were significantly heavier than birds trapped on other days, especially in Redstart, Blackbird, Song Thrush and Redwing (Table 5).

3.6. Weather and body condition of trapped birds

When comparing TWC of the morning before trapping between birds of average body condition and heavy/fat birds or light/lean birds, respectively, no clear relation between wind and body condition is apparent in the species studied (Fig. 1). The tendency for the heavy/fat fraction is to alight during headwinds in autumn, but during tailwinds in spring. No such trends are obvious for

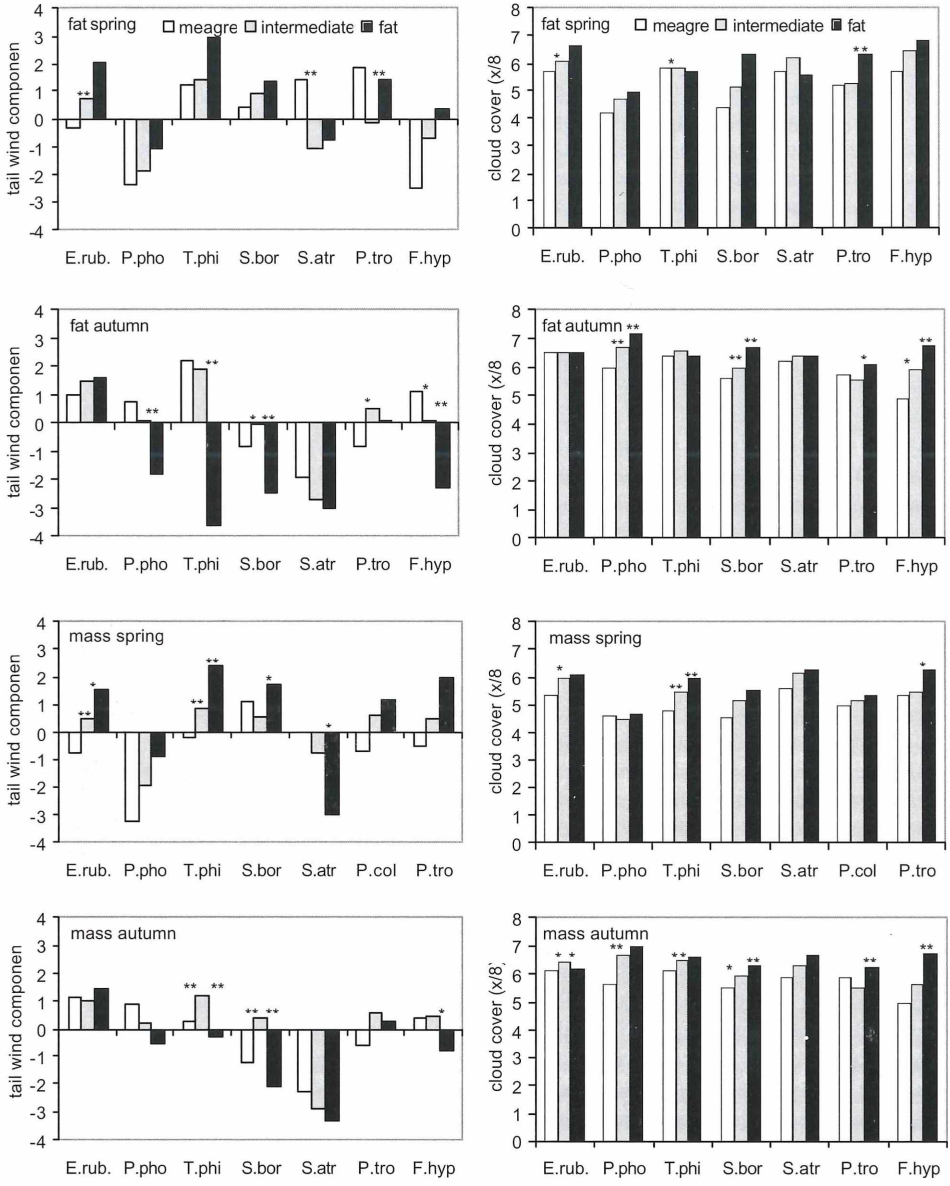
Table 5: Weather conditions and body mass of birds captured in the trapping garden during big falls of single species (> 1.5% of the grand total of the respective species form 1990 – 1999) and of the total of species (> 200 birds trapped per day). The number of cases is given for each category. Tailwind refers to positive and headwind to negaive TWC (see methods). Standardized body mass of big falls was compared with remaining days of the same season with birds judged as heavier or lighter if differences were significant (one-way ANOVA). Note that a given day can be a big fall for more than one species.

Tab. 5: Wetterbedingungen und Körpermasse von Vögeln aus Reusenfängen an Tagen mit Masseneinfall von einzelnen Arten (> 1,5% der Gesamtsumme der jeweiligen Art von 1990 – 1999) und an Tagen mit allgemeinem Masseneinfall (> 200 Vögel gefangen). Die Anzahl der aufgetretenen Fälle ist für jede Kategorie angegeben. Rückenwind bezieht sich auf positive, Gegenwind auf negative TWC-Werte (s. Methoden). Die standardisierte Körpermasse bei Masseneinfällen wurde mit der der anderen Tage der selben Zugperiode verglichen, wobei Vögel als leichter oder schwerer eingestuft wurden, wenn die Unterschiede signifikant waren (einfaktorielle ANOVA). Zu beachten ist, dass an einem Tag bei mehreren Arten ein Masseneinfall stattfinden kann.

	Precipation (mm)			tail-	head-	cloud cover		visibility		body mass at fall		
	< 1	1-5	> 5	wind	wind	0/8–6/8	7/8–8/8	> 2 km	< 2 km	> oth. days	= oth. days	< oth. days
spring migration												
Dunnock	3	0	0	2	1	1	2	3	0	0	2	1
Robin	6	1	0	5	2	1	6	7	0	1	6	0
Redstart	7	2	0	3	6	7	2	9	0	3	5	1
Blackbird	2	1	1	3	1	1	3	4	0	1	2	1
Song Thrush	1	0	0	1	0	0	1	1	0	1	2	1
Garden Warbler	6	1	0	7	0	4	3	7	0	2	4	1
Willow Warbler	4	0	0	2	2	2	2	4	0	0	4	0
total	**29**	**5**	**1**	**23**	**12**	**16**	**19**	**35**	**0**	**7**	**25**	**5**
big falls (> 200 birds)	14	3	1	15	3	7	11	18	0			
autumn migration												
Dunnock	7	1	0	8	0	2	6	7	1	0	6	2
Robin	6	1	0	7	0	0	7	7	0	3	4	0
Redstart	4	1	2	6	1	1	6	7	0	6	1	0
Blackbird	7	1	0	5	3	1	7	7	1	6	2	0
Song Thrush	6	1	2	7	2	0	9	9	0	4	2	2
Redwing	6	0	1	5	2	0	7	6	1	4	2	0
Garden Warbler	2	1	2	4	1	1	4	5	0	0	4	1
Blackcap	3	1	1	2	3	3	2	5	0	1	3	0
Willow Warbler	5	0	1	3	3	1	5	6	0	1	4	1
Pied Flycatcher	3	0	3	3	3	1	5	6	0	3	3	0
total	**49**	**7**	**12**	**50**	**18**	**10**	**58**	**65**	**3**	**28**	**31**	**6**
big falls (> 200 birds)	28	7	3	30	8	6	32	37	1			

Fig. 1: Average tail wind component and cloud cover in the morning before the capture of light/lean, intermediate and heavy/fat birds. See text for definition of groups. Significant differences compared to birds of intermediate body condition are marked with asteriscs (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ according to t-tests for TWC and Mann-Whitney-U-test for cloud cover). Note that negative values of TWC refer to headwinds.

Abb. 1: Durchschnittliche Rückenwindkomponente (TWC) und Bewölkungsgrade am Morgen vor dem Fang leichter/magerer, mittlerer und schwerer/fetter Vögel (Definitionen im Text). Signifikante Unterschiede im Vergleich zu Vögeln aus dem mittleren Bereich sind mit Sternen markiert (* $P < 0,05$, ** $P < 0,01$, *** $P < 0,001$ nach t-Tests für TWC und Mann-Whitney-U-Tests für Bewölkungsgrade).



light/lean birds. Considering another weather variable, the degree of cloud cover, in most species the trend was found that heavy/fat birds alight on mornings with more overcast than lighter birds (Fig1). Differences between the groups of body condition are significant only in a minority of cases in spring, but to a larger extend in autumn (Fig.1).

3.7 Body condition of tower kills

With respect to body mass and fat score, Willow Warblers collected on 1 May 1998 after hitting the lighthouse during nocturnal migration did not differ from birds mist-netted during early morning departure and caught in funnel traps during the day (Table 6). Song Thrushes killed at night at a telecommunication tower on 16 October 2000 were significantly lighter than conspecifics trapped during stopovers on the same day, but average fat scores were the same in both samples (Table 6).

Table 6: Body mass and fat score of Willow Warblers on 1 May 1998 and Song Thrushes on 16 October 2000, divided into birds killed at the lighthouse (Willow Warbler) or at a telecommunication tower (Song Thrush) during nocturnal migration, birds mist-netted in the Mittelland during early morning departure and birds caught in the trapping garden during the day. P-values refer to Mann-Whitney-U-tests between tower kills and departures (P_1) and tower kills and stopovers (P_2), respectively.

Tab. 6: Körpermassen und Fettstufen von Fitissen am 1. Mai 1998 und von Singdrosseln am 16. Oktober 2000, aufgeteilt nach während des nächtlichen Zuges an Leuchtturm (Fitis) und Telekom-Mast (Singdrossel) verunglückten Individuen, morgens aus dem Mittelland abziehenden Vögeln (Japannetzfänge) und tagsüber rastenden Vögeln (Reusenfänge im Fanggarten). P-Werte beziehen sich auf die Unterschiede zwischen verunglückten und abziehenden Vögeln (P_1) bzw. zwischen Anflugopfern und Rastvögeln (P_2) (Mann-Whitney-U-Tests).

	lighthouse or tower kills	early morning departures	stopovers	P_1	P_2
Willow Warbler 1 May 1998					
n	28	16	9		
BM_s	9.46	9.38	9.62	0.760	0.638
fat score	3.0	3.6	3.3	0.052	0.270
n	77		201		
BM_s	70.86		72.48		0.045
fat score	2.8		2.8		0.741

4. Discussion

Observations of passerine migration in the early morning hours showed that the number of migrants grounded on the small island of Helgoland is low on most days. As this happened also when many birds were seen migrating, weather conditions could have been good enough to leave aside a small stopover site and to complete the crossing of the German Bight. On other days, unfavourable weather could have led birds to avoid migration across the sea and to follow the coastline instead. At Helgoland, the migration pattern typical for most days seems to be that few birds cease their migratory flight in early morning, but arrivals throughout the day can fill up the island with migrants. This might be due to a decreasing tendency to continue sea crossings with deteriorating body condition as observed in the Mediterranean Sea (Bruderer & Liechti 1998). However, because many of the grounded birds depart from Helgoland after a quick stop the same day, the number of birds present on the island can also keep low. Such a pattern was described for Northern Wheatears on Helgoland (Delingat & Dierschke 2000), for Garden Warblers on small islands in the Mediterranean Sea (SPINA & PILASTRO 1999) and various passerine species on a barrier island at the northern edge of the Gulf of Mexico (KUENZI et al. 1991) and might reflect kind of dispersal in order to find suitable stopover habitats (see BRUDERER & JENNI 1988 and JENNI 1996 for comparable situations in high mountains and at an inland lake shore, repectively, and ALERSTAM 1978 for dispersal away from the coastline in the Baltic Sea). The ultimate reason for such a dispersal might be a high density of birds leading to interference during foraging, because it was shown for Pied Flycatchers and Northern Wheatears that settlement of migrants at a stopover site decreases with increasing density of conspecifics (VEIGA 1986, DIERSCHKE & DELINGAT 2001). A low amount of available food as possibly experienced during big falls with many competitors could lead to diurnal migratory activity, as measured in experimental birds with simulated stopover conditions without food (GWINNER et al. 1985). On Helgoland, arrivals and departures throughout the day also mean that nocturnal migrants can show diurnal migratory activity beyond the morning flights described from other sites (GAUTHREAUX 1978, BINGMAN 1980, WIEDNER et al. 1992).

In each migratory season, a handful of days is characterized by large numbers of passerines present already early in the morning. Most days with exceptional high trapping numbers showed good conditions for migration such as good visibility, tail winds and few or no precipitation (cf. RICHARDSON 1990). Therefore, high trapping numbers in most incidents seem to be a result of high numbers of birds migrating because of favourable flight conditions rather than an effect of adverse weather forcing birds to interrupt their flight. That many of these birds aloft during strong migration ceased their flight might be caused by orientational problems due to overcast which was noted on most days with big falls. These findings are in line with observations from the south coast of England, where in spring big falls of Willow Warblers coincided with favourable weather in the departure area (northern France) and solid overcast at the English coast (RIDDIFORD 1985). Overcast was shown to depress migratory departures of Robins from a Danish island (RABØL & HANSEN 1978), whereas bad visibility was the reason for big falls of passerines at another coastal site in England (LACK & LACK 1966). Another study comparing trapping numbers on Helgoland with meteorological data addressed supporting winds and overcast as the only factors leading to high numbers of passerines captured in the funnel traps (LANDES 1999). However, an earlier study denies an influence of wind conditions on bird migration on Helgoland (DINENDAHL 1954), and wind was found to be without importance for big fall incidents at an English coastal site, too (LACK & LACK 1966).

Body mass and fat scores of birds trapped on Helgoland were generally low compared to birds about to cross large ecological barriers (BIEBACH 1990, BAIRLEIN 1991). Possibly these low levels of body condition do not allow enough variation to show pronounced differences between birds departing in early morning and those stopping over all day. This might explain the low amount of diurnal variation of body condition within species found in this study. The hypothesis that early departing migrants should be in better condition than birds remaining on the island was confirmed in only a few cases, and even the differences found were biologically small. The relatively high body mass during big falls and the tendency to catch the heaviest fraction of birds with unfavourable wind and much overcast (both results obtained for autumn migration only) indicate that slight differences do actually exist between birds usually passing the stopover site and those usually using it. However, these differences are minor and of the same order of magnitude as for instance the increase of body mass during the day due to food intake as described elsewhere (CHERRY 1982, NORMAN 1987). Probably due to high bird densities and/or limited food supplies, passerines stopping over on Helgoland do not increase body mass in the first 1 – 4 days after arrival (RAISS 1976, DIERSCHKE in prep.). In addition, diurnal dynamics of body mass on Helgoland are probably hidden by an earlier departure of heavier birds and/or the later arrival of lighter birds (the latter possibly having flown a longer distance, cf. REDFERN et al. 2000). Nevertheless, further evidence for the lack of differences in body condition between birds migrating and those stopping over is given by two examples of birds killed at towers during nocturnal migration.

In conclusion, passerine birds do not appear to face major problems when migrating across a small ecological barrier, the German Bight - a distance easily covered within one night. As expected, the amount of fat deposits does not exceed the demands in most birds. This allows to keep transport costs and predation risk low, because a good manoeuvrability can be maintained to escape raptors and gulls which both occur as predators for migrating passerines in the southeastern North Sea (DIERSCHKE 2001a, 2001b). A probably only small fraction of migrants carries more reserves than necessary, but still does not reach levels as high as before crossing large ecological barriers (e.g. BIBBY & GREEN 1981 for Reed Warbler, BAIRLEIN 1991 for Garden Warbler). Because very fat individuals were never trapped on Helgoland, not even during big falls or with very unfavourable conditions for migration, it seems that maximum fat loads are only stored when actually needed. In this respect, trapped birds on Helgoland do not differ much from those at inland trapping stations, where birds carry low level fat reserves because the resulting flight range allows to reach other stopover sites (KAISER 1992). The species studied fit the pattern of little reserves carried during autumn migration in northern and central Europe with higher body mass occurring closer to the ecological barriers Mediterranean Sea and Sahara, as found for several species in a continent-wide analysis (SCHAUB & JENNI 2000). The only exception, the Sedge Warbler with much fat already during earlier stages of autumn migration (SCHAUB & JENNI 2000), was not included in this study because it is an uncommon visitor to Helgoland.

In conclusion, the decision of migrants to alight on a small island during the crossing of a small ecological barrier cannot be explained by a critical body condition, a result also found for passerines on small islands during migration across the Mediterranean Sea (SPINA & PILASTRO 1999). Perhaps landing at daytime is caused by an internal program reducing migratory activity after a period of flight or according to a diurnal pattern (BERTHOLD 1996). This would imply that the number of birds trapped is proportional to the number of birds aloft, a result currently found at the southern tip of Sweden (ZEHNDER & KARLSSON 2001). A study combining the estimation of volume of bird migration and the body condition of trapped birds could improve knowledge about the migration strategies of passerines during the crossing of the North Sea.

5. Zusammenfassung

Körperkondition ziehender Singvögel bei der Überquerung einer kleinen ökologischen Barriere.

Mit weniger als 150 km Distanz zwischen den umgebenden Küsten stellt die Deutsche Bucht (südöstliche Nordsee) für entlang einer Südwest-Nordost-Achse ziehende Singvögel nur eine kleine ökologische Barriere dar. Im Gegensatz zu Überquerungen größerer Barrieren (z.B. Sahara, Mittelmeer) trugen Singvögel, die auf der 50 km von der Küste entfernten Insel Helgoland gefangen wurden, nur geringe oder mittlere Fettreserven. Um herauszufinden, ob möglicherweise eine fettere, schwerere Fraktion von Zugvögeln die Insel überfliegt, ohne einen Rastaufenthalt einzulegen, wurden Singvögel in den frühen Morgenstunden mit Japannetzen gefangen. Im Helgoländer Mittelland findet morgens häufig ein Schleichzug statt, bei dem nachts oder in der Dämmerung eingefallene Vögel die Insel sofort wieder verlassen. Die Körperkondition unterschied sich zwischen diesen frühmorgens und den später am Tag gefangenen Vögeln im Allgemeinen nicht, signifikante Unterschiede waren in der Regel biologisch unbedeutend. Da damit zu rechnen ist, dass bei sehr ungünstigen Wetterbedingungen alle im Bereich Helgolands fliegenden Vögel die Gelegenheit zu einer (Not-)Landung nutzen, wurden die Beringungsdaten aus dem Fanggarten (drei große Trichterreusen) von Tagen mit Masseneinfall von Singvögeln gesondert betrachtet. Masseneinfälle gingen allerdings meist mit guten Flugbedingungen einher (mit Ausnahme meist vorhandener dichter Bewölkung). Nur auf dem Wegzug gab es bei einigen Arten einen Trend dahingehend, dass Vögel an Masseneinfalltagen schwerer waren als an den anderen Tagen der Zugperiode. In einem anderen Ansatz wurden die Wetterbedingungen beim Fang der schwersten und fettesten Individuen mit den Bedingungen beim Fang der im mittleren Bereich liegenden Vögel verglichen. Wiederum nur auf dem Wegzug gab es eine Tendenz, dass starke Gegenwinde und viel Bewölkung zum Fang (und damit zur Rast) von Vögeln führte, die schwerer/fetter als der Durchschnitt waren. Bei allen Ansätzen, auch beim Vergleich von nächtlichen Anflugopfern mit Fänglingen am nächsten Tag, gab es keine Anzeichen dafür, dass rastende Vögel generell in schlechte-

rer Kondition sind als über Helgoland hinwegziehende Artgenossen. Dies deutet darauf hin, dass für die Überquerung einer kleinen Barriere keine umfangreichen Fettreserven angelegt werden und dass bei einer kurzen Zugetappe die Körperkondition nicht das Landen in einem inselartigen Rastgebiet verursacht.

6. References

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