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Flight characteristics of birds: I. radar measurements of speeds

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This is the first part of a study on flight characteristics of birds and presents an annotated list of flight speeds of 139 western Palearctic species. All measurements were taken with the same tracking radar and corrected for wind influence according to radar-tracked wind-measuring balloons. Graphical presentation of the birds' air speeds emphasizes the wide variation of speeds within species and allows easy comparison between taxonomic groups, species, and types of flight. Unlike theoretical predictions, speeds increase only slightly with size. The larger species seem to be increasingly limited to speeds close to their speed of minimum power consumption V_{mp}. Released birds, apparently reluctant to depart with migratory speed, fly at considerably lower speeds than migrating conspecifics. While large birds seem to be limited to speeds around V_{mp}, smaller birds seem to be capable of selecting between various speeds, approaching predicted V_{mp} when tending to remain airborne at low cost, but flying at much higher speeds when tending to make best progress at low cost (around predicted speed of maximum range V_{mr}). Predictions of air speeds by aerodynamic models proved to be too low for small birds because the models do not account for the gain in speed attained by the reduction in profile drag during bounding flight of small passerines. The models predict excessive speeds for large birds because the power output available for flight seems to decline much more with size than previously assumed.

Flight performance is of critical importance to the fitness of birds. It depends on (1) group-specific life-history traits, (2) size-dependent morphological and physiological constraints, (3) adaptations to specific ecological niches and (4) on (often competing) requirements for migratory long-distance flights. Within given limits, the flight performance of a species varies with size, weight and wing length of individuals; it is modified according to the purpose and requirements of a particular flight and in reaction to environmental conditions.

Accordingly, measurements of flight speed will always reflect a species-specific component and modifications due to actual conditions. Separating the two is difficult and often depends on the judgement of the observer (e.g. with respect to the purpose of the observed flight). Due to drag, however, the rate of energy consumption in flight depends strongly on speed, and pressure to optimize speed is high. Thi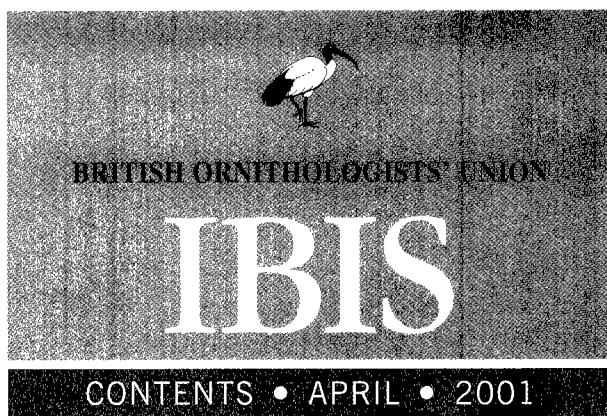s need allows some predictions about characteristic speeds of birds according to mass, wingspan, and wing area under defined conditions (Pennycuick 1969, 1975, 1978, 1989, Tucker 1973, Rayner 1979, 1986).

Hedenström and Alerstam (1995) evaluated and reviewed the criteria, constraints and other factors determining the optimal flight speeds of birds in different situations. In the present context only a few situations have to be considered, because we can assume that our measurements exclude feeding flights, transport flights, and aerial display. Most of our measurements comprise migratory flights, some are flights to roosting sites, and a few represent particular reactions after release. We will have to consider altitude, vertical speed, fuel load and wind as modifying factors, while drag reduction by formation flights can be excluded, because usually only single birds are involved.

In addition to the numerous factors involved in the selection of flight speeds, there are great difficulties inherent in measuring it. Thus, it is hardly surprising that published bird speed records show little coherence. Rayner (1985) suggested that because many inaccurate methods had been used and wind conditions were rarely taken into account, published

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records, such as those of Meinertzhagen (1955) were often misleading and inaccurate. Even recent text books (Bezzel & Prinzinger 1990) report some highly questionable speeds without reference.

Recognizing this gap in knowledge as well as the great importance of making realistic assumptions on flight speeds for calculations of flight range and energy consumption in migratory flights, the need for reliable speed measurements is obvious. As a by-product of three decades of tracking-radar studies of bird migration (Bruderer 1999), a database of speed measurements has been built up, comprising thousands of individual tracks of identified birds with wind measurements at the birds' flight altitudes.

This paper aims to describe and discuss the high intraspecific variability of speeds and provide realistic estimates of typical flight speeds, allowing meaningful interspecific comparisons. Our own radar measurements of visually identified individuals and of some small bird flocks are presented and discussed with respect to variation due to the situation of the birds and the environmental conditions. The paper is intended to replace less reliable collections of data such as those of Meinertzhagen (1955); in most cases it provides the reader with the possibility to judge these and other measurements. The measured speeds will be compared with speeds predicted by aerodynamic theory. A brief introduction to aerodynamic theory is given at the beginning of the section on measured speeds and models of optimal flight speed.

METHODS AND MATERIALS

Observation periods and sites

Since 1968 the tracking radar 'Superfledermaus' has been used by the Swiss Ornithological Institute to observe bird migration (Bruderer 1969, 1971, 1999). Emphasis was on nocturnal migration, but increasingly observations on diurnal migration were included, paralleled by an increasing interest in identified birds.

In order to make this overview as comprehensive as possible, data from all the observation periods carried out by the Swiss Ornithological Institute are included in this evaluation (see list in Bruderer 1999). In 20 out of the 30 years of the period 1968 to 1997, observations were made mainly during the autumn migration (August to October), fewer during spring migration (March to May), some to record winter movements (November to February), and a few in July to compare roosting and migrating Swifts *Apus apus*. 15 observation sites in different parts of Switzerland, four in

southern Germany, two in southern Israel (Arava Valley and Negev Highlands), and two in the western Mediterranean (Mallorca and Malaga) were used to study different aspects of bird migration and flight behaviour. The percentage of tracks recorded in the different areas reflects the duration of observation periods and the increasing interest in identified species in recent projects: Central Europe Lowlands (400-600 m asl) 13.8%, Alps (~1800 m asl) 2.5%, Israel (–150 to 450 m asl) 56.4%, western Mediterranean (sea level) 27.3%.

Tracking system and recorded data

'Superfledermaus' is an ex-military fire-control radar with about 3.3 cm wavelength, 150 kW peak pulse power, 2.2° nominal beam width, and 0.3 µs pulse length. Tracking is achieved by the beam conically scanning around the optical axis of the parabolic antenna with an offset of 1°, and by a moving distance gate (for details see Bloch *et al.* 1981). The minimum distance for detection is about 100 m, maximum range for tracking a single Chaffinch *Fringilla coelebs* in tail-on view (i.e. with minimal radar cross-section) is 4 to 4.5 km. The nominal tracking accuracy is 0.06° in azimuth and elevation and ±10 m in distance.

While the tracking system remained the same over the years, the recording system was continuously improved. In the early days, positions of tracked birds were recorded by taking photographs of the radar's instruments every 20 seconds (Bruderer 1971); transition to electronic recording and digital analysis of 20 s intervals was achieved in the mid-1970s (Bloch *et al.* 1981); in 1980 digital recording on PC was introduced, with data points being registered every second, and 10 to 20 points being approximated by a regression line to provide average flight data over 10 to 20 seconds (Bruderer *et al.* 1995).

In all cases the system provided data on the birds' altitude, ground speed, vertical speed, and flight direction. Winds at ground level were measured by hand-held or mounted anemometers, upper winds by tracking pilot balloons. The birds' heading and air speed were calculated by subtracting the wind vector at the corresponding flight level from the vector of the birds' track. In the early observation periods the time difference between wind-measurement and a single bird track could be up to 6 h, while later the frequency of wind-measurements was increased, so that the difference was stepwise reduced to less than 3 h and finally less than 2 h (wind-measurements every 4 h). In spite of these frequent wind-measurements, the calcu-

lation of air speeds using time-shifted wind data may be a source of error. This error is, however, small compared to other published flight speed data, which only rarely are combined with on-site wind-measurements.

The 'Superfledermaus' radar allows visual identification of tracked birds by a telescope (12.4×) mounted parallel to the axis of the parabolic antenna. In some cases, such as swifts, the recorded wing-beat pattern of the birds allows identification to the species-level even at night (Bruderer & Weitnauer 1972, Stark & Liechti 1993). In the present study, however, only visually identified birds have been included. In some explicitly stated cases radar-identified targets were considered for comparison.

Selection of data, flight phases and atmospheric conditions

Initially all the flight path data of identified birds were included in the database. In most cases the data refer to tracks of individual birds, but data of small flocks (up to five birds) were included. In a few explicitly mentioned cases we included flocks of up to ten individuals. Wind data for the corresponding height were added and used to calculate air speed and heading. In a further step, flight paths with high vertical speed (exceeding ± 2 m/s) and/or deviating from straight flight were excluded. This means that for soaring birds no soaring phases were included.

Diurnal migrants were usually tracked during migratory passage flights. Diurnal residents were recorded during long straight flights, such as flights to roosts or distant feeding sites, where they can be supposed to use an economic flight speed to cover the given distance, but may accelerate when trying to catch up with a preceding flock (e.g. Althaus & Bruderer 1982). Birds migrating by day and night, such as Starlings *Sturnus vulgaris* and Skylarks *Alauda arvensis*, were tracked during diurnal flights (considered to be migratory). The reader should be aware of the difference between resident species (R) and migrants in migratory (M) and non-migratory (m) flights; the corresponding letters are added to the names in the list of species.

Nocturnal migrants could not be identified in normal migratory flights; accordingly, even extreme migrants were marked 'm' instead of 'M'. For most of them it was not possible to record long diurnal flights. The only possibility to obtain flight data of such species was to catch and release them at dusk or equipped with a tiny light (mini gelatine capsule filled with Cyalume) at night. When they made the transition to straight horizontal flight, we hoped that they

would go over to migratory flight. However, the speeds of released birds were often considerably lower than comparable birds in free flight. It seems that most released birds need some time to get oriented and to decide whether to look for a landing place or initiate a migratory flight. Therefore, the data of released birds are presented separately, marked with a vertical bar.

Soaring migrants are problematic, because the speed of migration is the cross-country speed, including soaring and gliding phases, while straight flights are usually gliding flights, which are increasingly supported by wing-flaps as thermal conditions deteriorate. Horizontal flapping flights are the basis of theoretical calculations of optimal flight speeds; however, in large soaring birds they occur only rarely and do not correspond to migratory speeds. Small raptor species, such as harriers, sparrowhawks and falcons, may use both soaring and flapping flight. To cope with this problem in soaring birds, we provide one table for flapping fliers (including small raptors and large soaring birds in powered flight) and another for soaring birds. In the table on soaring birds we emphasize the speeds used in the straight phases of economic migratory flights (gliding and/or flap-gliding). Vertical winds, which are not accounted for in this study, are a source of error in the measured speeds, because there is a close relationship between vertical and horizontal speeds; soaring birds can glide faster and need less support by flapping when the birds get support by extended updrafts (Spaar & Bruderer 1996).

The lists would have been excessively long if we separated different locations, altitudes, and wind conditions. As a compromise we provide the 'true' air speed graphically and calculate the 'equivalent' air speed at sea level for comparison according to theoretical predictions. The difference between true and equivalent air speed gives an indication of the difference between the air density at the measuring altitude and sea level. In addition we give the range of true ground speeds (allowing a rough judgement of wind influence in the given sample) and the average vertical speed (to indicate reduced or increased speeds due to climb and descent).

Input data for predictions on flight speeds

Theoretical predictions of flight speeds are based on models such as those of Pennycuick (1989, 1992). Such general models attempt to predict certain aspects of performance for flying animals, based on estimates of body mass, wingspan, wing area, and assumed drag coefficients, which may vary with speed (Pennycuick

1995). Adjustments in the assumed drag coefficient (Pennycuick 1996) produce considerable changes in the calculated speeds (see also Fig. 2). All the default values were used as suggested by Pennycuick (1989, 1992). Body mass, wingspan and wing area are subject to individual variation and, therefore, produce additional variation in the results.

The original data used in this study are shown in Table 1. Most body masses were taken from Bauer and Glutz (1966-69), Glutz and Bauer (1980–82, 1985–97), and Glutz *et al.* (1971–73, 1975–77). Whenever possible, we took the average weights indicated for migrating birds. Missing data were added (in the following priority) following Dunning (1993) and

Table 1. Body mass, wingspan, and wing area of the species included in the analysis. Sources: (1) Glutz von Blotzheim *et al.* (1966–97), (2) Cramp *et al.* (1977–94), (3) Dunning (1993), (4) Meinertzhagen & Basel Museum (unpubl. data), (5) Spaar & Bruderer (1997a), details are given in the text.

Species	Mass (kg)	Wing span (m)	Wing area (m²)	Species	Mass (kg)	Wing span (m)	Wing area (m²)
Phalacrocorax carbo	3.000 (1)	1.450 (2)	0.2494 (4)	*Pterocles coronatus*	0.300 (3)	0.565 (2)	0.0432 (4)
Pelecanus onocrotalus	10.000 (1)	3.150 (2)	1.0196 (4)	*Pterocles senegallus*	0.260 (1)	0.590 (2)	0.0449 (4)
Nycticorax nycticorax	0.560 (1)	1.085 (2)	0.1600 (4)	*Pterocles orientalis*	0.410 (3)	0.715 (2)	0.0721 (4)
Ardeola ralloides	0.290 (1)	0.860 (2)	0.1114 (4)	*Columba livia*	0.350 (1)	0.665 (2)	0.0649 (4)
Egretta alba	1.000 (1)	1.550 (2)	0.2356 (4)	*Columba palumbus*	0.500 (1)	0.775 (2)	0.0904 (4)
Ardea cinerea	1.600 (1)	1.850 (2)	0.3979 (4)	*Streptopelia senegalensis*	0.088 (4)	0.425 (2)	0.0304 (4)
Ardea purpurea	0.970 (1)	1.350 (2)	0.2488 (4)	*Cuculus canorus*	0.120 (1)	0.575 (2)	0.0508 (4)
Ciconia nigra	3.000 (1)	1.500 (2)	0.2842 (4)	*Asio flammeus*	0.350 (1)	1.025 (2)	0.1343 (4)
Ciconia ciconia	3.070 (1)	1.600 (2)	0.5808 (4)	*Caprimulgus ruficollis*	0.069 (3)	0.665 (2)	0.0567 (4)
Plegadis falcinellus	0.630 (1)	0.875 (2)	0.0986 (4)	*Apus melba*	0.105 (1)	0.570 (2)	0.0304 (4)
Platalea leucorodia	1.900 (1)	1.225 (2)	0.2341 (4)	*Apus apus*	0.044 (1)	0.450 (2)	0.0170 (4)
Phoenicopterus ruber	3.000 (1)	1.525 (2)	0.2715 (4)	*Apus pallidus*	0.042 (3)	0.440 (2)	0.0263 (4)
Anas platyrhynchos	1.140 (1)	0.895 (2)	0.1015 (4)	*Merops apiaster*	0.058 (1)	0.465 (2)	0.0273 (4)
Anas acuta	0.910 (1)	0.875 (2)	0.0918 (4)	*Upupa epops*	0.070 (1)	0.440 (2)	0.0422 (4)
Anas querquedula	0.380 (1)	0.615 (2)	0.0588 (4)	*Lullula arborea*	0.027 (1)	0.285 (2)	0.0164 (4)
Mergus merganser	1.480 (1)	0.895 (2)	0.0680 (4)	*Alauda arvensis*	0.036 (1)	0.330 (2)	0.0194 (4)
Pernis apivorus	0.900 (1)	1.300 (4)	0.2364 (4)	*Riparia riparia*	0.014 (1)	0.278 (2)	0.0096 (4)
Elanus caeruleus	0.200 (1)	0.810 (2)	0.0899 (4)	*Ptyonoprogne rupestris*	0.024 (1)	0.333 (2)	0.0113 (4)
Milvus migrans	0.830 (1)	1.700 (2)	0.2805 (4)	*Hirundo rustica*	0.021 (1)	0.333 (2)	0.0133 (4)
Milvus milvus	1.100 (1)	1.850 (2)	0.3803 (4)	*Hirundo daurica*	0.022 (1)	0.330 (2)	0.0154 (4)
Haliaeetus albicilla	4.800 (1)	2.200 (2)	0.6151 (4)	*Delichon urbica*	0.018 (1)	0.275 (2)	0.0107 (4)
Neophron percnopterus	1.900 (1)	1.675 (2)	0.3555 (4)	*Anthus trivialis*	0.022 (1)	0.260 (2)	0.0126 (4)
Gyps fulvus	7.000 (1)	2.600 (2)	0.9889 (4)	*Anthus pratensis*	0.017 (1)	0.235 (2)	0.0108 (4)
Torgos tracheliotus	7.500 (3)	2.725 (2)	0.8162 (4)	*Motacilla flava*	0.017 (1)	0.250 (2)	0.0103 (4)
Aegypius monachus	9.000 (1)	2.725 (2)	0.9588 (4)	*Motacilla alba*	0.021 (1)	0.275 (2)	0.0127 (4)
Circaetus gallicus	1.700 (1)	1.900 (2)	0.4058 (4)	*Prunella modularis*	0.020 (1)	0.200 (2)	0.0092 (4)
Circus aeruginosus	0.600 (1)	1.225 (2)	0.2248 (4)	*Erithacus rubecula*	0.017 (1)	0.210 (2)	0.0095 (4)
Circus cyaneus	0.430 (1)	1.100 (2)	0.1539 (4)	*Phoenicurus ochruros*	0.016 (1)	0.245 (2)	0.0106 (4)
Circus macrourus	0.380 (1)	1.075 (2)	0.1553 (4)	*Phoenicurus phoenicurus*	0.016 (1)	0.223 (2)	0.0099 (4)
Circus pygargus	0.300 (1)	1.125 (2)	0.1463 (4)	*Saxicola rubetra*	0.017 (1)	0.225 (2)	0.0095 (4)
Accipiter gentilis	1.100 (1)	1.500 (2)	0.2564 (4)	*Oenanthe oenanthe*	0.024 (1)	0.290 (2)	0.0137 (4)
Accipiter nisus	0.200 (1)	0.625 (2)	0.0700 (4)	*Monticola saxatilis*	0.050 (1)	0.350 (2)	0.0204 (4)
Accipiter brevipes	0.220 (1)	0.700 (2)	0.0739 (4)	*Turdus merula*	0.094 (1)	0.363 (2)	0.0280 (4)
Buteo buteo buteo	1.000 (1)	1.205 (2)	0.2404 (4)	*Turdus pilaris*	0.100 (1)	0.405 (2)	0.0318 (4)
Buteo buteo vulpinus	0.579 (5)	1.188 (5)	0.2070 (5)	*Turdus philomelos*	0.089 (1)	0.345 (2)	0.0214 (4)
Buteo rufinus	1.200 (1)	1.370 (2)	0.3281 (4)	*Turdus viscivorus*	0.109 (1)	0.448 (2)	0.0358 (4)
Aquila pomarina	1.300 (1)	1.465 (2)	0.5153 (4)	*Acrocephalus palustris*	0.012 (1)	0.195 (2)	0.0066 (4)
Aquila nipalensis	2.900 (1)	2.025 (2)	0.4853 (4)	*Acrocephalus scirpaceus*	0.012 (1)	0.190 (2)	0.0062 (4)
Aquila heliaca	3.100 (1)	2.000 (2)	0.4815 (4)	*Acrocephalus arundinaceus*	0.031 (1)	0.265 (2)	0.0117 (4)
Aquila chrysaetos	4.400 (1)	2.120 (2)	0.5237 (4)	*Hippolais icterina*	0.014 (1)	0.223 (2)	0.0081 (4)
Hieraaetus pennatus	0.800 (1)	1.105 (2)	0.2004 (4)	*Hippolais polyglotta*	0.011 (1)	0.188 (2)	0.0061 (4)
Hieraaetus fasciatus	2.000 (1)	1.650 (2)	0.3792 (4)	*Sylvia hortensis*	0.021 (1)	0.225 (2)	0.0105 (4)
Pandion haliaetus	1.500 (1)	1.575 (2)	0.3125 (4)	*Sylvia curruca*	0.012 (1)	0.185 (2)	0.0073 (4)
Falco naumanni	0.150 (1)	0.650 (2)	0.0611 (4)	*Sylvia communis*	0.016 (1)	0.208 (2)	0.0073 (4)
Falco tinnunculus	0.210 (1)	0.755 (2)	0.0684 (4)	*Sylvia borin*	0.020 (1)	0.223 (2)	0.0093 (4)

continued

Table 1. continued.

Species	Mass (kg)	Wing span (m)	Wing area (m²)	Species	Mass (kg)	Wing span (m)	Wing area (m²)
Falco vespertinus	0.165 (1)	0.720 (2)	0.0728 (4)	*Sylvia atricapilla*	0.020 (1)	0.215 (2)	0.0089 (4)
Falco subbuteo	0.215 (1)	0.870 (2)	0.0950 (4)	*Phylloscopus trochilus*	0.009 (1)	0.193 (2)	0.0070 (4)
Falco eleonorae	0.360 (1)	1.200 (2)	0.0509 (4)	*Regulus regulus*	0.006 (1)	0.145 (2)	0.0046 (4)
Falco concolor	0.250 (3)	0.975 (2)	0.1196 (4)	*Regulus ignicapillus*	0.006 (1)	0.145 (2)	0.0050 (4)
Falco biarmicus	0.700 (1)	1.025 (2)	0.1418 (4)	*Muscicapa striata*	0.015 (1)	0.243 (2)	0.0110 (4)
Falco peregrinus	0.800 (1)	1.025 (2)	0.1328 (4)	*Ficedula hypoleuca*	0.013 (1)	0.238 (2)	0.0091 (4)
Falco pelegrinoides	0.510 (1)	0.900 (2)	0.1102 (4)	*Parus major*	0.019 (1)	0.240 (2)	0.0106 (4)
Alectoris chukar	0.560 (1)	0.495 (2)	0.0582 (4)	*Lanius collurio*	0.030 (1)	0.255 (2)	0.0145 (4)
Grus grus	5.000 (1)	2.325 (2)	0.6157 (4)	*Garrulus glandarius*	0.180 (1)	0.550 (2)	0.0595 (4)
Cursorius cursor	0.115 (1)	0.540 (2)	0.0407 (4)	*Corvus monedula*	0.230 (1)	0.705 (2)	0.0768 (4)
Glareola pratincola	0.080 (1)	0.625 (2)	0.0503 (4)	*Corvus frugilegus*	0.450 (1)	0.900 (2)	0.1373 (4)
Glareola nordmanni	0.100 (1)	0.640 (2)	0.0540 (4)	*Corvus corone*	0.610 (1)	0.985 (2)	0.1577 (4)
Charadrius hiaticula	0.065 (1)	0.525 (2)	0.0207 (4)	*Corvus ruficollis*	0.720 (4)	1.160 (2)	0.1944 (4)
Vanellus vanellus	0.210 (1)	0.845 (2)	0.0820 (4)	*Corvus corax*	1.200 (1)	1.350 (2)	0.2472 (4)
Calidris alpina	0.047 (1)	0.405 (2)	0.0156 (4)	*Sturnus vulgaris*	0.080 (1)	0.395 (2)	0.0224 (4)
Philomachus pugnax	0.160 (1)	0.530 (2)	0.0429 (4)	*Fringilla coelebs*	0.021 (1)	0.265 (2)	0.0124 (4)
Gallinago gallinago	0.110 (1)	0.455 (2)	0.0271 (4)	*Fringilla montifringilla*	0.022 (1)	0.255 (2)	0.0125 (4)
Numenius arquata	0.780 (1)	0.900 (2)	0.1189 (4)	*Serinus serinus*	0.011 (1)	0.215 (2)	0.0076 (4)
Tringa ochropus	0.085 (1)	0.590 (2)	0.0289 (4)	*Carduelis chloris*	0.027 (1)	0.260 (2)	0.0112 (4)
Actitis hypoleucos	0.058 (1)	0.395 (2)	0.0244 (4)	*Carduelis carduelis*	0.016 (1)	0.233 (2)	0.0088 (4)
Larus ridibundus	0.280 (1)	1.050 (2)	0.0946 (4)	*Carduelis spinus*	0.013 (1)	0.215 (2)	0.0072 (4)
Larus canus	0.380 (1)	1.200 (2)	0.1209 (4)	*Carduelis cannabina*	0.018 (1)	0.233 (2)	0.0093 (4)
Larus fuscus	0.770 (1)	1.425 (2)	0.2430 (4)	*Carduelis flammea*	0.011 (1)	0.225 (2)	0.0083 (4)
Larus cachinnans	1.150 (1)	1.490 (2)	0.2496 (4)	*Emberiza hortulana*	0.023 (1)	0.260 (2)	0.0138 (4)
Chlidonias leucopterus	0.068 (1)	0.650 (2)	0.0545 (4)				

Meinertzhagen (unpubl. data see below). Wingspans were taken from Cramp *et al.* (1977-1994). Wing areas were taken from the (unpublished) data set of Meinertzhagen stored in the bird collection of the British Museum (Natural History) at Tring. As Meinertzhagen measured the area of one wing by a planimeter and doubled this area to obtain the wing area, we had to add the area of the body between the wing bases to obtain the surface required for Pennycuick's model calculations. Having measured the depth of the wings at their bases in Meinertzhagen's collection, we measured the body width of mounted birds or 'naturally' stuffed skins in the Museum of Natural History in Basel, being aware that the effect of inaccuracies in these measurements on calculated speeds is not very important (Table 2).

Table 2. Variation of V_{mp} (speed of minimum power) and V_{mr} (speed of maximum range) with air density ρ, body mass *M*, wingspan *b*, and wing area *S* calculated according to the model of Pennycuick (1992) based on our species sample (Table 1).

	Variation (%)					
	+ 10%	+ 5%	+ 1%	−1%	−5%	−10%
Δρ						
V_{mp}	−4.67%	−2.43%	−0.56%	+ 0.45%	+ 2.62%	+ 5.32%
V_{mr}	−4.43%	−2.27%	−0.39%	+ 0.50%	+ 2.51%	+ 5.20%
corresponding height change (m)	− 1021	− 511	− 104	+ 105	+ 531	+ 1083
ΔM						
V_{mp}	+ 8.23%	+ 3.37%	+ 1.70%	−1.82%	−3.69%	−9.76%
V_{mr}	+ 7.35%	+ 3.06%	+ 1.58%	−1.54%	−3.15%	−8.44%
Δb						
V_{mp}	−4.66%	−2.43%	−0.56%	+ 0.45%	+ 2.61%	+ 5.32%
V_{mr}	−6.44%	−3.37%	−0.71%	+ 0.77%	+ 3.87%	+ 8.28%
ΔS						
V_{mp}	+ 0.00%	+ 0.00%	+ 0.00%	−0.00%	−0.00%	−0.00%
V_{mr}	+ 1.50%	+ 0.75%	+ 0.20%	−0.14%	−0.71%	−1.44%

Estimates of errors in calculations

Table 2 provides an idea of the influence of varying input data on the outcome of theoretical speed predictions according to Pennycuick (1992), using the species sample of this study. The definitions of the theoretical speeds (e.g. V_{mp} and V_{mr}) are given at the beginning of the section 'Measured speeds and models of optimal flight speed'. Calculating equivalent air speeds at sea level from the true air speeds recorded at various altitudes led to a reduction of the average air speed over all data by 3.1%; the maximum reduction in birds flying above the Alps was 20%. A variation in air density of ±10% (equivalent to a change in altitude of about 1100 m) led to a variation in mean V_{mp} and V_{mr} of roughly ±5%. A variation in body mass of ±10% induced a variation in mean V_{mp} of about ±3.5% and ±3% in V_{mr}. A variation of ±10% in wing span corresponds to roughly ±5% variation in V_{mp} and ±7% in V_{mr}. A corresponding variation in wing area proved to have no relevant influence on V_{mp} while mean V_{mr} varied by slightly more than ±1%. The species means of air speeds showed no relevant shift when either all tracks were included or the data sets were restricted to tracks recorded within 90, 60 and 30 minutes from the next wind measurement, respectively.

MEASURED FLIGHT SPEEDS

The lists of flight speeds (Tables 3 & 4) follow Snow and Perrins (1998) with respect to English names and taxonomic order. In three cases, two generic names are given in the species' account, while the commonly used names (*Egretta, Apus, Ptyonoprogne*) are retained in the list. The air speed V_a ('true' on site air speed) is shown graphically as a point if only a mean speed of one flight phase was available; mean and range are given if two to four flight phases were available; mean with standard error, standard deviation and range are given if more than four flight phases were available. The graphical presentation of the data intentionally avoids exact numbers and the reader may recognize intra-specific variation on the horizontal axis and look for inter-specific comparison and different flight types on the vertical axis. Equivalent air speed EqV_a at sea level was calculated from the original data to allow

comparison with theoretical predictions. In the column V_{mp} (V_{mr}) Pennycuick, we included the theoretical minimum power and maximum range speeds calculated according to Pennycuick (1992; program 1, version 1.1; all default values as suggested by the author, air density at sea level; parameters of the birds according to Table 1). The range of the corresponding ground speeds V_g provides a rough indication of wind influence. V_z is the average vertical speed of the birds in the sample considered. The number of flight phases indicates the sample size used for the statistical calculations. A flight phase is either a complete radar track (in most birds with flapping flight) or a section of a track with unchanged flight behaviour (in most soaring birds a straight flight between two soaring phases). In many flapping birds the number of tracks and flight phases is the same, while in soaring birds there are often two or three flight phases per track. The number of flight phases and tracks in combination with the total length of observation time in seconds allow a judgement of the reliability of the data.

Flight speeds of flapping fliers

The table on flapping fliers comprises 121 species, 84 of which are based on free-flying birds, 28 on released individuals, nine species comprise data of free-flying and released birds. In the latter nine cases as well as for two additional species (*Motacilla flava, Carduelis spinus*), two lines per species are given to separate information on obviously differing flight behaviour. Soaring birds are included if information on pure 'powered flight' was available. Powered flight was assumed when the individual in question was beating its wings more or less continuously and V_z was ≥ 0.

Flight speeds of soaring birds in straight flight

The table on soaring birds comprises 30 species, 18 of which are not included in Table 3. Various speeds are indicated for each species, corresponding with particular circumstances. The straight flights of soaring birds with less than ± 2 m/s vertical speed were split, as far as available, into three flight types: gliding flight without wing flaps (=), 'flapping flight' with a relatively high proportion of wing flaps (~), and mixed behav-

Table 3. Specific flight speeds. The letter specifies the type of flight: **M** = migrants in (assumed) migratory flight, **m** = migrants assumed not to be in migratory flight, **R** = residents. Released birds are marked with a bold bar (|) at the end of the box with the name. For further explanation to the following column headings (**air speed V_a, EqV_a ± sd, V_{mp} (V_{mr}) Pennycuick, V_g, V_z, flight phases (tracks)** and **observ time**) see text. For air speed V_a a point alone indicates the mean speed of one flight phase; mean and range (fine line) are given if two to four flight phases were available; standard deviation (medium line) and standard error (bold line) are given if more than four flight phases were available. *see over*

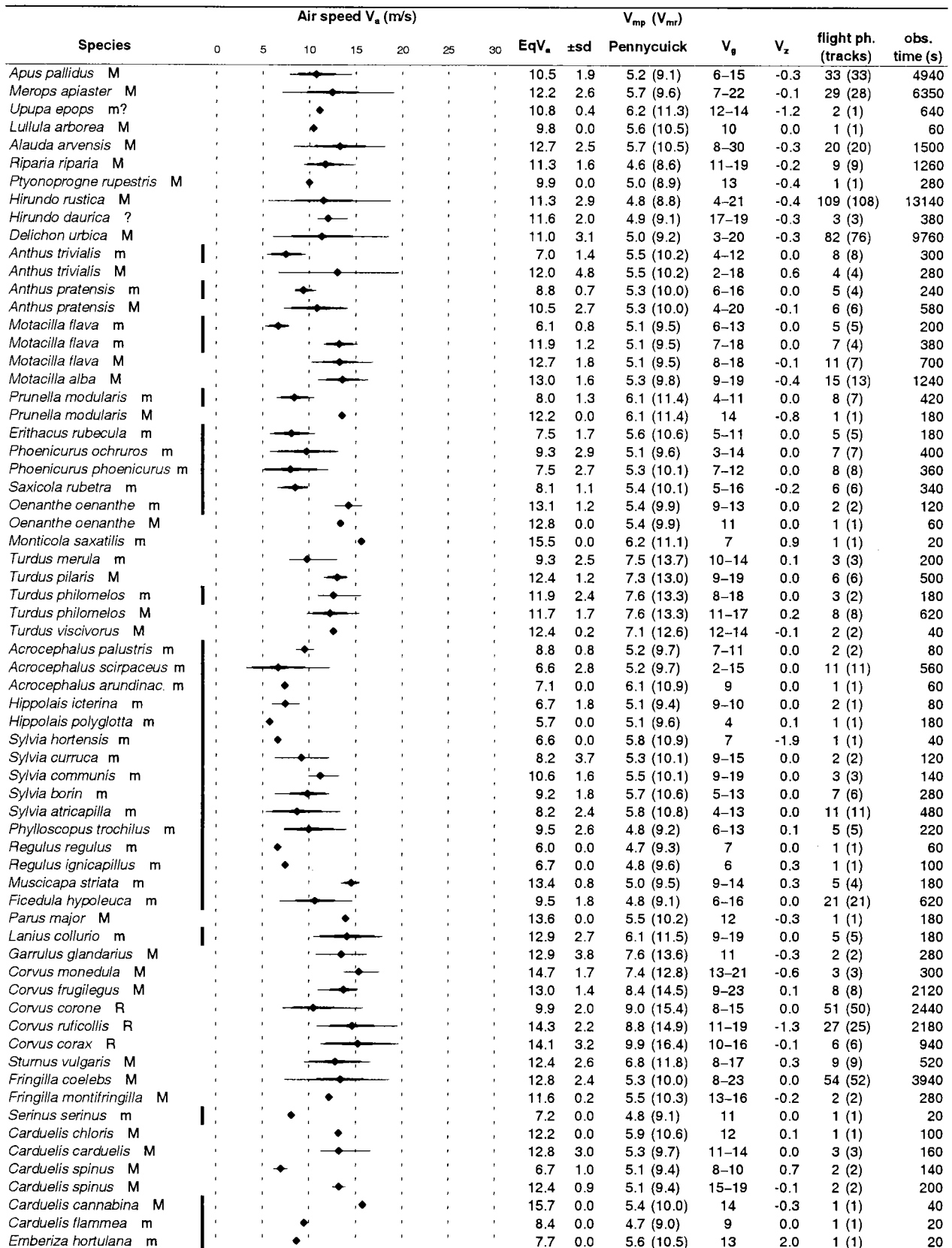| Species	Air speed V_a (m/s)	V_{mp} (V_{mr})					
	0 5 10 15 20 25 30	EqV$_a$	±sd	Pennycuick	V$_g$	V$_z$	flight ph. (tracks)	obs. time (s)
Phalacrocorax carbo m		16.7	3.3	13.5 (21.4)	12–17	0.1	2 (2)	900
Nycticorax nycticorax M		11.2	0.5	8.3 (13.7)	8–16	0.0	4 (4)	2140
Ardeola ralloides M		11.7	0.0	7.3 (12.3)	13	0.1	1 (1)	480
Egretta alba M		10.2	1.1	8.6 (13.6)	12–19	0.0	3 (2)	1000
Ardea cinerea M		11.2	1.6	9.4 (15.2)	7–24	0.0	52 (49)	12240
Ardea purpurea M		10.8	2.0	9.1 (15.0)	3–20	0.1	12 (12)	5660
Ciconia ciconia M		9.1	1.2	12.9 (23.0)	11–18	0.8	3 (3)	250
Plegadis falcinellus M		12.6	1.7	9.6 (15.6)	13–18	-0.3	6 (5)	1280
Platalea leucorodia M		14.1	1.4	12.4 (20.6)	11–23	0.0	10 (7)	2280
Phoenicopterus ruber M		15.2	2.7	13.1 (20.9)	13–24	0.1	3 (3)	620
Anas platyrhynchos Rm?		21.4	2.4	11.9 (19.1)	18–24	0.3	8 (7)	680
Anas acuta m		13.3	0.9	11.0 (17.7)	18–21	1.1	2 (2)	540
Anas querquedula m		14.1	0.0	9.5 (15.9)	16	0.8	1 (1)	360
Mergus merganser m		21.2	0.0	13.1 (20.0)	18	-0.1	1 (1)	40
Pernis apivorus M		10.2	1.5	9.0 (15.0)	8–14	0.4	15 (15)	3020
Elanus caeruleus ?		15.3	0.0	6.5 (11.0)	17	0.2	1 (1)	320
Milvus migrans M		11.5	1.3	7.7 (12.3)	11–20	0.8	2 (2)	150
Neophron percnopterus R		10.5	0.0	10.6 (17.1)	14	0.0	1 (1)	60
Circus aeruginosus M		9.7	1.1	8.0 (13.5)	8–18	0.3	16 (15)	2720
Circus macrourus M		8.5	0.0	7.2 (12.0)	15	0.4	1 (1)	240
Accipiter nisus M		9.8	1.3	7.4 (12.9)	7–13	0.2	57 (47)	5870
Accipiter brevipes M		10.8	2.3	7.3 (12.3)	8–20	0.2	22 (18)	4650
Buteo buteo buteo M?		9.6	1.7	9.8 (16.5)	7–16	0.4	68 (57)	3980
Buteo buteo vulpinus M		11.1	0.0	8.0 (13.4)	7	0.8	1 (1)	70
Aquila heliaca R		9.5	0.9	11.6 (18.6)	13–14	0.0	2 (1)	280
Pandion haliaetus M		11.4	1.6	10.0 (16.2)	10–14	0.4	10 (10)	3660
Falco naumanni M		11.3	2.8	6.6 (11.2)	8–18	-0.6	17 (12)	4430
Falco tinnunculus m		7.6	0.0	6.9 (11.3)	8	0.0	1 (1)	60
Falco tinnunculus Mm		12.3	2.5	6.9 (11.3)	4–20	-0.7	168 (152)	27160
Falco vespertinus M		12.8	1.0	6.5 (10.9)	12–17	-0.8	6 (4)	970
Falco subbuteo M		11.3	2.2	6.5 (10.8)	6–18	-0.5	20 (20)	5910
Falco eleonorae M		12.8	2.3	6.7 (10.0)	12	-0.3	2 (2)	550
Falco concolor ?		15.2	1.9	6.5 (10.8)	12–20	-0.8	5 (5)	460
Falco biarmicus R		11.1	2.7	9.2 (15.2)	11–17	-0.7	3 (3)	650
Falco peregrinus M		12.1	3.5	9.7 (15.8)	7–21	-0.5	15 (13)	3050
Falco pelegrinoides R		14.4	0.1	8.8 (14.4)	14–17	-1.0	2 (2)	350
Alectoris chukar R		14.2	0.0	12.2 (22.0)	18	0.2	1 (1)	140
Cursorius cursor R		15.1	2.8	6.6 (11.1)	12–16	-0.3	4 (4)	520
Glareola pratincola ?		12.1	1.6	5.4 (9.4)	12–18	0.1	8 (8)	1460
Glareola nordmanni ?		11.3	1.9	5.8 (9.9)	9–16	0.4	5 (4)	1100
Charadrius hiaticula m		10.6	0.0	5.5 (8.9)	11	-0.6	1 (1)	40
Vanellus vanellus M		11.9	2.0	6.5 (10.7)	9–17	0.3	3 (2)	280
Calidris alpina m		8.9	1.6	5.7 (9.3)	8–11	0.3	2 (2)	80
Philomachus pugnax M		13.6	1.2	7.4 (12.6)	14–18	0.2	3 (3)	760
Gallinago gallinago ?		15.5	0.0	7.1 (11.7)	18	0.0	1 (1)	360
Numenius arquata ?		13.2	1.2	10.3 (17.0)	14–15	0.8	2 (2)	180
Tringa ochropus m		5.8	2.0	5.7 (9.3)	3	-0.2	2 (2)	60
Tringa ochropus m		22.7	0.0	5.7 (9.3)	20	-1.9	1 (1)	260
Actitis hypoleucos m		9.1	3.6	6.1 (10.6)	3–8	0.5	2 (2)	40
Larus ridibundus Rm		11.2	3.0	6.5 (10.4)	6–20	-0.5	15 (15)	980
Larus canus M?		11.1	0.0	6.8 (10.8)	14	-0.2	1 (1)	160
Larus fuscus M		11.9	2.2	8.1 (13.3)	9–18	-0.4	11 (11)	3020
Larus cachinnans R		14.0	2.8	9.3 (14.8)	2–28	-0.6	239 (239)	20040
Chlidonias leucopterus M		12.0	0.0	5.1 (8.8)	17	0.0	1 (1)	320
Pterocles coronatus R		16.9	0.0	9.1 (14.9)	17	0.0	1 (1)	100
Pterocles senegallus R		18.4	0.0	8.4 (13.8)	17	0.1	1 (1)	120
Pterocles orientalis R		18.3	0.5	9.1 (15.0)	18–20	-0.2	2 (2)	120
Columba livia R		17.5	2.0	8.9 (14.7)	11–23	0.1	39 (39)	3880
Columba palumbus M		17.6	3.2	9.4 (15.6)	14–27	-0.1	11 (11)	880
Streptopelia senegalensis R		11.5	0.0	6.8 (11.8)	13	-0.7	1 (1)	60
Cuculus canorus m		10.4	0.0	6.5 (11.1)	12	0.0	1 (1)	60
Asio flammeus ?		8.4	1.4	7.1 (11.9)	4–12	0.2	3 (3)	3380
Caprimulgus ruficollis m		8.9	0.0	5.0 (8.8)	10	-0.3	1 (1)	80
Apus melba M		12.6	2.9	6.2 (10.1)	8–18	-0.7	38 (36)	6380
Apus apus m		9.2	0.2	5.2 (8.6)	11–12	0.0	2 (2)	120
Apus apus M		10.6	3.0	5.2 (8.6)	2–21	-0.1	172 (163)	13440

Species	Air speed V_a (m/s)	EqV_a	±sd	V_{mp} (V_{mr}) Pennycuick	V_θ	V_z	flight ph. (tracks)	obs. time (s)
Apus pallidus M		10.5	1.9	5.2 (9.1)	6–15	-0.3	33 (33)	4940
Merops apiaster M		12.2	2.6	5.7 (9.6)	7–22	-0.1	29 (28)	6350
Upupa epops m?		10.8	0.4	6.2 (11.3)	12–14	-1.2	2 (1)	640
Lullula arborea M		9.8	0.0	5.6 (10.5)	10	0.0	1 (1)	60
Alauda arvensis M		12.7	2.5	5.7 (10.5)	8–30	-0.3	20 (20)	1500
Riparia riparia M		11.3	1.6	4.6 (8.6)	11–19	-0.2	9 (9)	1260
Ptyonoprogne rupestris M		9.9	0.0	5.0 (8.9)	13	-0.4	1 (1)	280
Hirundo rustica M		11.3	2.9	4.8 (8.8)	4–21	-0.4	109 (108)	13140
Hirundo daurica ?		11.6	2.0	4.9 (9.1)	17–19	-0.3	3 (3)	380
Delichon urbica M		11.0	3.1	5.0 (9.2)	3–20	-0.3	82 (76)	9760
Anthus trivialis m		7.0	1.4	5.5 (10.2)	4–12	0.0	8 (8)	300
Anthus trivialis M		12.0	4.8	5.5 (10.2)	2–18	0.6	4 (4)	280
Anthus pratensis m		8.8	0.7	5.3 (10.0)	6–16	0.0	5 (4)	240
Anthus pratensis M		10.5	2.7	5.3 (10.0)	4–20	-0.1	6 (6)	580
Motacilla flava m		6.1	0.8	5.1 (9.5)	6–13	0.0	5 (5)	200
Motacilla flava m		11.9	1.2	5.1 (9.5)	7–18	0.0	7 (4)	380
Motacilla flava M		12.7	1.8	5.1 (9.5)	8–18	-0.1	11 (7)	700
Motacilla alba M		13.0	1.6	5.3 (9.8)	9–19	-0.4	15 (13)	1240
Prunella modularis m		8.0	1.3	6.1 (11.4)	4–11	0.0	8 (7)	420
Prunella modularis M		12.2	0.0	6.1 (11.4)	14	-0.8	1 (1)	180
Erithacus rubecula m		7.5	1.7	5.6 (10.6)	5–11	0.0	5 (5)	180
Phoenicurus ochruros m		9.3	2.9	5.1 (9.6)	3–14	0.0	7 (7)	400
Phoenicurus phoenicurus m		7.5	2.7	5.3 (10.1)	7–12	0.0	8 (8)	360
Saxicola rubetra m		8.1	1.1	5.4 (10.1)	5–16	-0.2	6 (6)	340
Oenanthe oenanthe m		13.1	1.2	5.4 (9.9)	9–13	0.0	2 (2)	120
Oenanthe oenanthe M		12.8	0.0	5.4 (9.9)	11	0.0	1 (1)	60
Monticola saxatilis m		15.5	0.0	6.2 (11.1)	7	0.9	1 (1)	20
Turdus merula m		9.3	2.5	7.5 (13.7)	10–14	0.1	3 (3)	200
Turdus pilaris M		12.4	1.2	7.3 (13.0)	9–19	0.0	6 (6)	500
Turdus philomelos m		11.9	2.4	7.6 (13.3)	8–18	0.0	3 (2)	180
Turdus philomelos M		11.7	1.7	7.6 (13.3)	11–17	0.2	8 (8)	620
Turdus viscivorus M		12.4	0.2	7.1 (12.6)	12–14	-0.1	2 (2)	40
Acrocephalus palustris m		8.8	0.8	5.2 (9.7)	7–11	0.0	2 (2)	80
Acrocephalus scirpaceus m		6.6	2.8	5.2 (9.7)	2–15	0.0	11 (11)	560
Acrocephalus arundinac. m		7.1	0.0	6.1 (10.9)	9	0.0	1 (1)	60
Hippolais icterina m		6.7	1.8	5.1 (9.4)	9–10	0.0	2 (1)	80
Hippolais polyglotta m		5.7	0.0	5.1 (9.6)	4	0.1	1 (1)	180
Sylvia hortensis m		6.6	0.0	5.8 (10.9)	7	-1.9	1 (1)	40
Sylvia curruca m		8.2	3.7	5.3 (10.1)	9–15	0.0	2 (2)	120
Sylvia communis m		10.6	1.6	5.5 (10.1)	9–19	0.0	3 (3)	140
Sylvia borin m		9.2	1.8	5.7 (10.6)	5–13	0.0	7 (6)	280
Sylvia atricapilla m		8.2	2.4	5.8 (10.8)	4–13	0.0	11 (11)	480
Phylloscopus trochilus m		9.5	2.6	4.8 (9.2)	6–13	0.1	5 (5)	220
Regulus regulus m		6.0	0.0	4.7 (9.3)	7	0.0	1 (1)	60
Regulus ignicapillus m		6.7	0.0	4.8 (9.6)	6	0.3	1 (1)	100
Muscicapa striata m		13.4	0.8	5.0 (9.5)	9–14	0.3	5 (4)	180
Ficedula hypoleuca m		9.5	1.8	4.8 (9.1)	6–16	0.0	21 (21)	620
Parus major M		13.6	0.0	5.5 (10.2)	12	-0.3	1 (1)	180
Lanius collurio m		12.9	2.7	6.1 (11.5)	9–19	0.0	5 (5)	180
Garrulus glandarius M		12.9	3.8	7.6 (13.6)	11	-0.3	2 (2)	280
Corvus monedula M		14.7	1.7	7.4 (12.8)	13–21	-0.6	3 (3)	300
Corvus frugilegus M		13.0	1.4	8.4 (14.5)	9–23	0.1	8 (8)	2120
Corvus corone R		9.9	2.4	9.0 (15.4)	8–15	0.0	51 (50)	2440
Corvus ruficollis R		14.3	2.2	8.8 (14.9)	11–19	-1.3	27 (25)	2180
Corvus corax R		14.1	3.2	9.9 (16.4)	10–16	-0.1	6 (6)	940
Sturnus vulgaris M		12.4	2.6	6.8 (11.8)	8–17	0.3	9 (9)	520
Fringilla coelebs M		12.8	2.4	5.3 (10.0)	8–23	0.0	54 (52)	3940
Fringilla montifringilla M		11.6	0.2	5.5 (10.3)	13–16	-0.2	2 (2)	280
Serinus serinus m		7.2	0.0	4.8 (9.1)	11	0.0	1 (1)	20
Carduelis chloris M		12.2	0.0	5.9 (10.6)	12	0.1	1 (1)	100
Carduelis carduelis M		12.8	3.0	5.3 (9.7)	11–14	0.0	3 (3)	160
Carduelis spinus M		6.7	1.0	5.1 (9.4)	8–10	0.7	2 (2)	140
Carduelis spinus M		12.4	0.9	5.1 (9.4)	15–19	-0.1	2 (2)	200
Carduelis cannabina M		15.7	0.0	5.4 (10.0)	14	-0.3	1 (1)	40
Carduelis flammea m		8.4	0.0	4.7 (9.0)	9	0.0	1 (1)	20
Emberiza hortulana m		7.7	0.0	5.6 (10.5)	13	2.0	1 (1)	20

Table 4. List of flight speeds of soaring birds. Flapping flight (~), gliding flight (=), mixed behaviour (=~), cross-country speed (cc, travelling speed relative to the air taken from Spaar 1997). Column headings as in Table 3, for further explanations see text.

Species	Air speed V_a (m/s)	EqV$_a$	±sd	V Pennycuick	V$_g$	V$_z$	flight phases (tracks)	observ time (s)
Pelecanus onocrotalus M ~		15.6	0.0	13.6	17	-0.8	1 (1)	60
Pelecanus onocrotalus M =~		16.0	1.7	13.6	14–23	-1.0	9 (5)	1170
Ciconia nigra M ~		16.0	1.8	13.2	12–22	-1.0	6 (6)	670
Ciconia nigra M =~		15.4	2.2	13.2	8–20	-1.0	28 (21)	5020
Ciconia ciconia M ~		13.9	2.9	12.9	9–20	-1.0	27 (26)	2550
Ciconia ciconia M =~		13.5	2.5	12.9	6–22	-0.9	113 (109)	15820
Pernis apivorus M =		14.2	2.6	16.5	7–27	-1.0	311 (234)	41790
Pernis apivorus M ~		10.1	1.5	9.0	8–14	0.4	16 (16)	3160
Pernis apivorus M =~		12.1	2.9	9.0	4–22	-0.5	177 (125)	60570
Pernis apivorus M cc							80	
Milvus migrans M =		13.3	2.3	16.1	3–20	-0.8	105 (60)	12930
Milvus migrans M ~		11.7	1.3	7.7	9–20	-0.2	8 (7)	1320
Milvus migrans M =~		12.1	2.9	7.7	4–22	-0.6	86 (49)	18090
Milvus migrans M cc							24	
Milvus milvus M =		14.8	0.9	16.5	14–17	-1.1	4 (3)	430
Milvus milvus M =~		10.1	2.3	8.2	7–21	-0.3	19 (19)	3200
Haliaeetus albicilla ? =~		13.1	0.0	12.8	13	-1.0	1 (1)	560
Neophron percnopterus R =		15.6	2.3	18.3	8–25	-1.0	118 (93)	15880
Neophron percnopterus R ~		12.6	2.5	10.6	12–14	-0.3	3 (3)	380
Neophron percnopterus R =~		15.7	1.9	10.6	10–22	-1.2	48 (19)	7760
Neophron percnopterus R cc							26	
Gyps fulvus R =		16.0	2.6	21.2	9–25	-0.7	122 (77)	13860
Gyps fulvus R =~		16.5	2.2	13.3	10–26	-0.6	48 (23)	4860
Gyps fulvus R cc							13	
Torgos tracheliotus R =		16.1	0.8	21.7	13–16	-0.2	3 (1)	390
Torgos tracheliotus R =~		11.8	0.0	13.3	14	-1.2	1 (1)	100
Aegypius monachus R =~		15.5	0.0	14.2	14	0.3	1 (1)	700
Circaetus gallicus M? =		13.6	2.2	17.9	7–21	-0.5	70 (34)	10310
Circaetus gallicus M? =~		13.4	2.3	9.5	8–19	-0.6	58 (31)	7150
Circaetus gallicus M? cc							9	
Circus aeruginosus M =		12.6	2.0	15.0	6–19	-0.7	78 (50)	9950
Circus aeruginosus M ~		10.1	2.0	8.0	8–18	0.0	23 (22)	4520
Circus aeruginosus M =~		11.6	2.1	8.0	6–24	-0.6	72 (4)	20300
Circus aeruginosus M cc							11	
Circus cyaneus M =		11.7	1.5	14.6	10–15	-1.2	3 (3)	560
Circus cyaneus M =~		11.4	1.1	7.4	13–25	-1.3	4 (3)	580
Circus macrourus M =		13.2	4.0	14.3	9–18	-1.2	11 (5)	1080
Circus macrourus M ~		9.6	1.0	7.2	15–16	0.1	3 (3)	700
Circus macrourus M =~		12.9	1.1	7.2	9–16	-1.0	12 (7)	1960
Circus pygargus M =		12.4	1.9	13.9	10–18	-0.9	22 (10)	2840
Circus pygargus M ~		8.4	0.5	6.4	8–11	-0.4	2 (1)	330
Circus pygargus M =~		10.7	2.1	6.4	8–16	-0.3	31 (23)	11280
C. pygargus/macrourus M cc							12	
Accipiter gentilis R =~		9.7	0.0	9.1	9	-0.2	1 (1)	180
Accipiter nisus M =		10.9	1.3	13.0	9–14	-0.5	66 (65)	13060
Accipiter nisus M ~		10.0	1.8	7.4	7–18	0.1	67 (64)	7500
Accipiter nisus M =~		11.5	2.2	7.4	6–20	-0.5	31 (25)	6580
Accipiter brevipes M =		13.3	2.3	13.4	6–21	-1.1	76 (44)	9810
Accipiter brevipes M ~		11.1	2.1	7.3	8–20	-0.3	64 (57)	13390
Accipiter brevipes M =~		11.4	2.4	7.3	7–20	-0.8	126 (91)	17870
Accipiter brevipes M cc							28	
Buteo buteo buteo M? =		11.5	1.4	16.4	9–15	-0.6	93 (93)	21960
Buteo buteo buteo M? ~		9.6	1.7	9.8	7–16	0.4	68 (68)	3980
Buteo buteo buteo M? =~		11.0	3.4	9.8	4–18	-0.3	23 (23)	4960
Buteo buteo vulpinus M =		14.4	2.4	14.9	6–27	-0.9	549 (324)	65770
Buteo buteo vulpinus M ~		13.3	1.3	8.0	7–17	-0.6	15 (13)	1940
Buteo buteo vulpinus M =~		14.4	2.4	8.0	7–23	-1.0	242 (51)	35950
Buteo buteo vulpinus M cc							129	
Buteo rufinus M? =		14.6	2.8	16.7	8–20	-1.1	15 (11)	1870
Buteo rufinus M? =~		14.8	2.4	9.8	9–23	-1.0	35 (17)	3450

Species	Air speed V_a (m/s)	EqV$_a$	±sd	V Penny-cuick	V$_g$	V$_z$	flight phases (tracks)	observ time (s)
Aquila pomarina M =		14.5	2.7	16.2	6–22	-0.6	145 (67)	16630
Aquila pomarina M ~		11.7	3.0	9.8	12–13	-0.6	2 (2)	520
Aquila pomarina M =~		14.7	2.0	9.8	8 - 21	-0.8	41 (9)	6800
Aquila pomarina M cc							25	
Aquila nipalensis M =		14.3	2.5	19.5	5–28	-0.5	242 (101)	29030
Aquila nipalensis M ~		7.7	1.0	11.3	10–12	-0.7	4 (1)	370
Aquila nipalensis M =~		15.3	2.0	11.3	10–26	-1.1	41 (9)	7880
Aquila nipalensis M cc							38	
Aquila heliaca R =~		9.5	0.9	11.6	13–14	0.0	2 (1)	280
Aquila chrysaetos R =		15.1	1.7	20.5	12–16	-0.7	3 (2)	260
Aquila chrysaetos R =~		13.0	6.2	12.6	4–23	-0.2	9 (7)	2100
Hieraaetus pennatus M =		13.8	2.7	15.9	7–27	-0.5	54 (25)	6540
Hieraaetus pennatus M ~		11.3	1.7	9.4	7–14	-0.1	2 (2)	290
Hieraaetus pennatus M =~		12.5	3.1	9.4	5–19	-0.4	32 (21)	8710
Hieraaetus pennatus M cc							13	
Hieraaetus fasciatus M? =		11.0	2.2	18.6	9–20	0.5	3 (2)	180
Hieraaetus fasciatus M? =~		14.0	1.5	10.9	12–15	-1.0	2 (2)	560
Pandion haliaetus M =		12.5	1.7	17.6	11–18	-0.5	14 (11)	1720
Pandion haliaetus M ~		11.4	1.6	10.0	10–14	0.4	10 (10)	3660
Pandion haliaetus M =~		13.7	2.6	10.0	5–20	-0.7	28 (21)	11650
Grus grus M ~		13.6	0.0	12.6	15	-1.2	1 (1)	250
Grus grus M =~		14.5	1.6	12.6	14–25	-0.4	28 (14)	6940

iour, gliding supported by occasional wing flaps (~=); the flight type is indicated by the corresponding signature in the list of species. The speed of gliding flights depends mainly on thermal conditions, allowing steeper, and thus faster glides when good updrafts are available (Schmid *et al.* 1986, Liechti *et al.* 1996, Spaar 1995, 1996, 1997, Spaar & Bruderer 1996, 1997a, 1997b), this being the main source of scatter in the data. Pure flapping flight is only rarely used because it is an uneconomic flight for such large birds; speeds may be close to the theoretical speed of minimum power V_{mp} (see Table 3). In the column V Pennycuick we indicate calculated V_{mp} for individuals in flapping flight or mixed behaviour. For individuals in pure gliding flight we indicate optimal gliding speed at maximum cross-country speed when climb rate is 2 m/s. For those species where Spaar (1997) provided a value for cross-country speed (including thermal circling and gliding phases), we also included these values to indicate average speeds on migration over long distances (marked by cc; no theoretical equivalent indicated).

Species accounts (comments and comparison with other publications)

Some of the speed measurements listed in the two tables call for additional explanation and discussion, if possible in comparison with other published data and to comment on the validity of our own data. The general problems discussed above concerning methods of registration, data evaluation and analysis, as well as

flight behaviour and intra-individual variation have always to be remembered, but will not be considered in every case. To achieve optimal comparability we provide the original values of V_a and the calculated EqV_a for comparison.

Reference to older measurements and to compilations based on such measurements are generally avoided; however, we refer to older data if our measurements seem to be biased, e.g. by release effects, and no more recent data are available for comparison. Data on Nearctic species have been shown if no appropriate data for the Palearctic species are available. The papers of our own working group (e.g. Bruderer & Weitnauer 1972, Althaus & Bruderer 1982, Bruderer & Neusser 1982, Schmid *et al.* 1986, Bruderer *et al.* 1994, Liechti *et al.* 1996, Spaar 1995, 1997) deal with parts of the same data set as the present study and are therefore only mentioned if they provide important additional explanations. Stark (1996) included additional data on nocturnal migrants identified according to wing-beat pattern and phenology. General references for the migratory speeds of nocturnal migrants, classified according to wing-beat pattern, are available in Bloch *et al.* (1981), Bloch and Bruderer (1982), Liechti (1992), Liechti and Bruderer (1995), and Bruderer (1997a). The speeds calculated according to the model of Pennycuick (1992) are not discussed in the species account, because Pennycuick's model seems generally to underestimate the speeds of small birds and to overestimate those of large birds (Tables 3 & 4; Welham 1994). These problems are discussed

later (see section on measured speeds and models of optimal flight speed).

Cormorant *Phalacrocorax carbo*: 17.4/16.7 (V_a/EqV_a) are realistic values for economic flight. Pennycuick (1997) gives 15.4 m/s for the smaller Shag *P. aristotelis*.

White Pelican *Pelecanus onocrotalus*: 15.8/15.6 m/s (flapping) and 16.3/16.0 m/s (flap-gliding) both slightly sinking are typical migratory speeds between thermals. Pennycuick (1997) reports 10.1 m/s for Brown Pelicans *P. occidentalis* in sustained horizontal flapping or flapping-gliding non-migratory flight at low level, which may be close to V_{mp}.

Night Heron *Nycticorax nycticorax*: The speeds of four flights (11.9/11.2 m/s) are in the same range as in other herons.

Squacco Heron *Ardeola ralloides*: Despite its much lower body mass, the only recorded individual had an air speed (12.0/11.7 m/s) similar to other herons. Corroborating data on air speeds of small Ardeidae from America are provided by Tucker and Schmidt-Koenig (1971): Little Blue Heron *Egretta caerulea* (11.6 m/s), Snowy Egret *Egretta thula* (12.0 m/s). Pennycuick (1997) gives a very low value of 8.8 m/s for the Snowy Egret in non-migratory flight at low level (close to V_{mp}?).

Great White Egret *Egretta alba/Casmerodius albus*: The measured air speed (12.5 m/s) and the EqV_a (10.2 m/s) show the maximum calculated reduction in a species mean due to altitude. Comparison with other herons suggests that realistic values may be somewhere in the middle, i.e. that the calculated reduction may go too far. Tucker and Schmidt-Koenig (1971) provide a value of 10.8 m/s, which is lower than their measurements for the smaller Blue and Snowy Egrets.

Grey Heron *Ardea cinerea*: The well documented mean (11.9/11.2 m/s) is astonishingly close to that of smaller herons. Tucker and Schmidt-Koenig (1971) measured 14.3 m/s for the similarly sized Great Blue Heron *Ardea herodias*. Pennycuick (1997), on the other hand, found 9.4 m/s (close to V_{mp}?) for this American species in non-migratory flight at low level.

Purple Heron *Ardea purpurea*: The mean air speed of 11.2/10.8 m/s is slightly lower than that of all other herons, but well documented by 12 tracks and 94 min tracking.

Black Stork *Ciconia nigra*: 16.5/16.0 m/s (flapping) and 15.7/15.4 m/s (flap-gliding) at average sinking rates of 1 m/s are slightly higher than in *C. ciconia* and are typical migratory speeds between thermals.

White Stork *Ciconia ciconia*: 14.4/13.9 m/s (flapping) and 13.9/13.5 m/s (flap-gliding) at average sinking rates of 1 m/s are typical for migrating birds between

thermals. The wide variation in air speeds (6.6 to 20 m/s) under various conditions is discussed by Liechti *et al.* (1996). Some tracks in powered flight resulted in an average of 9.8/9.1 m/s.

Glossy Ibis *Plegadis falcinellus*: 13.0/12.6 m/s are reasonable migratory speeds.

Spoonbill *Platalea leucorodia*: In spite of a wide variation in ground speeds, all the birds flew with air speeds between 13.7 and 16.7 m/s, resulting in an average migratory speed of 15.05/14.1 m/s.

Greater Flamingo *Phoenicopterus ruber*: The averages of 15.9/15.2 m/s are realistic migratory speeds. Two small flocks (four and five individuals) migrating at heights of 1020 and 1290 m above ground in southern Israel flew at air speeds of 19.1 and 14.9 m/s, respectively. A group of four birds was tracked on a non-migratory flight 100 m above the Salinas of Mallorca at a speed of 13.7 m/s. All birds were continuously flapping.

Mallard *Anas platyrhynchos*: The observed air speeds in the range of 17.6 and 24.4 m/s (mean 22.0/21.4 m/s) are very high; these individuals were not migrating and are perhaps not representative for the species. The value of 20.7 m/s for the slightly lighter Gadwall *Anas strepera* reported by Tucker and Schmidt-Koenig (1971) provides some support for our measurements.

Pintail *Anas acuta*: The speed of 13.6/13.3 m/s is low; the birds were climbing at a rate of 1.1 m/s and not migrating. The 16.6 m/s (18.4 in headwind, 15.5 in tailwind) reported by Tucker and Schmidt-Koenig (1971) are based on 16 individuals or flocks; even those flying with light tail wind had air speeds higher than our average. These speeds are more representative than our measurements.

Garganey *Anas querquedula*: The relatively low speed (14.4/14.1 m/s) is realistic, considering that the bird was climbing at a rate of 0.8 m/s. In horizontal flight we expect slightly higher speeds.

Goosander *Mergus merganser*: The observed air speed of 21.8/21.2 m/s is high, but realistic for a species with high wing-loading; it is, however, only represented by one individual during 40 s. Rydén and Källander (1964) report ground speeds of 19.5 m/s.

Honey Buzzard *Pernis apivorus*: Like most raptors, the Honey Buzzard varied greatly in air speed, ranging from 5.3 to over 24 m/s. The wide variation in gliding (average 14.6/14.2 m/s) and flap-gliding (average 12.6/12.1 m/s) depends on environmental conditions (Bruderer *et al.* 1994). In powered flight the average was reduced to 10.8/10.2 m/s. Cross-country speed was 9.5 m/s. Other soaring raptor species react similarly to environmental conditions, but average gliding

speed is positively correlated with the species' body mass (Spaar 1997).

Black-winged Kite *Elanus caeruleus*: One individual showed an astonishingly high air speed of 16.5/15.3 m/s in horizontal flapping flight (climb rate 0.18 m/s).

Black Kite *Milvus migrans*: The average speed in powered flight was 11.9/11.5 m/s, while average gliding and flap-gliding speeds were 13.6/13.3 and 12.5/12.1 m/s, respectively; cross-country speed averaged 9.2 m/s.

Red Kite *Milvus milvus*: Four gliding individuals in Israel showed average air speeds of 15.1/14.8 m/s, while a good sample with mixed flight behaviour from Europe varied around 10.5/10.1 m/s.

White-tailed Eagle *Haliaeetus albicilla*: The speed in flap-gliding flight (13.7/13.1 m/s) is intermediate between the speeds of other eagles in flapping and in gliding flight. Pure flapping speed is probably lower. Pennycuick (1997) gives 11.2 m/s for the similarly sized Bald Eagle *H. leucocephalus* in flapping flight.

Egyptian Vulture *Neophron percnopterus*: Most birds were tracked in gliding flights or mixed flight behaviour in good thermal conditions resulting in high averages of 16.1/15.7 m/s. Three individuals from Israel in powered flight varied around 12.9/12.6 m/s. Cross-country speed was 10.2 m/s. Pennycuick (1997) gives a very low speed for non-migratory flapping flight in the American Black Vulture *Coragyps atratus* (10.8 m/s).

Griffon Vulture *Gyps fulvus*: Average gliding and flap-gliding speeds of 16.5/16.0 and 17.0/16.5 m/s are reasonable compared to other large vultures. Cross-country averages 10 m/s.

Lappet-faced Vulture *Torgos tracheliotus*: Only two tracks from southern Israel are available. Three flight phases of three gliding individuals varied around 16.2/16.1 m/s, while an individual with mixed behaviour (which was only 100 m over ground and had a sink rate of 1.2 m/s) showed an air speed of only 11.8/11.8 m/s. It seems that the air speeds of vultures are not strongly correlated with body mass, but rather depend on environmental conditions and the purpose of the flight (see Egyptian and Griffon Vultures; Spaar 1997).

Black Vulture *Aegypius monachus*: A group of six individuals gliding northward with some intermittent wing flaps from the southern tip of Mallorca at an air speed of 16.1/15.5 m/s compares well with other similarly sized vultures.

Short-toed Eagle *Circaetus gallicus*: 13.6/13.4 m/s (flapping-gliding), 13.8/13.6 m/s (gliding), and 10 m/s (cross-country speed) are close to similar species under comparable conditions.

Marsh Harrier *Circus aeruginosus*: 10.5/10.1 in flapping flight, 12.0/11.6 m/s in flap-gliding, and 13.0/12.7 m/s while gliding compare well with the other *Circus* species. Cross-country speed is 8.2 m/s. The migratory flight strategies of Marsh, Montagu's and Pallid Harriers are documented by Spaar and Bruderer (1997b).

Hen Harrier *Circus cyaneus*: The harrier with the smallest sample size. However, its gliding (11.8/11.7 m/s) and flap-gliding (11.6/11.4 m/s) speeds fit well into the very homogeneous harrier group.

Pallid Harrier *Circus macrourus*: Variation of speeds was typically wide, averaging at 13.6/13.2 m/s for gliding and 13.2/12.9 for flap-gliding. Continuous flapping resulted in 9.9/9.6 m/s, and 8.6/8.5 m/s if restricted to positive flight angles, respectively.

Montagu's Harrier *Circus pygargus*: The smallest of the observed harrier species fits well into the whole group with average gliding and flap-gliding speeds of 12.7/12.4 and 11.1/10.7 m/s, respectively, and the lowest flapping speed within the genus (8.7/8.4 m/s). Cross-country speed of *Circus pygargus/macrourus* is 7.5 m/s.

Goshawk *Accipiter gentilis*: Goshawks showed typical intermittent gliding phases at average speeds of 10.1/9.7 m/s. Pennycuick *et al.* (1994) found 15.5 m/s in an individual trained to chase a lure-rabbit on the ground. Horizontal hunting flights higher up may be even faster, as suggested by a Goshawk holding the same speed as a feral pigeon *Columba livia domestica* over about 5 min, but not reducing the distance to the prey (pers. obs.). Alerstam (1986) measured 13.9 m/s in a bird gliding off after soaring to initiate a stoop. Highest diving speed was in the range of 28-30 m/s.

Sparrowhawk *Accipiter nisus*: The speeds of the usual flap-gliding flight of this species varied around 12.1/11.5 m/s. Horizontal flapping flights resulted in speeds around 10.5/10.0 m/s. Slow gliding speed was 11.5/10.9 m/s.

Levant Sparrowhawk *Accipiter brevipes*: Flap-gliding flights varied around 11.6/11.4 m/s (similar to *A. nisus*), flapping flights around 11.4/11.1, while gliding flights (some of them in very good thermal conditions in southern Israel) showed wide variation around a mean of 13.6/13.3 m/s. Speeds of powered flight varied around 11.1/10.8 m/s. Nocturnally migrating individuals, identified according to wing-beat pattern provided average flap-gliding air speeds of 9.6 m/s in autumn under average tailwinds of 5.3 m/s; nocturnal migrants in spring, facing side and opposing winds (average 6.3 m/s) had air speeds around 11.3 m/s

(Spaar *et al.* 1998). Thus, even with no assistance by thermals and absolutely horizontal flight ($V_z = \pm 0.5$ m/s), the air speed may vary by 15% due to following or opposing winds. Cross-country speed was 9.5 m/s.

Common Buzzard *Buteo buteo buteo*: The mean speed of powered flight was 10.1/9.6 m/s. Gliding and flap-gliding speeds varied around 12.1/11.5 and 11.5/11.0 m/s, respectively. Similar to the situation mentioned for *Pernis apivorus* the migrating Buzzards in central Europe have often to cope with poor thermal conditions. Schmid *et al.* (1986) measured mean gliding speeds of 12.2 m/s in September and 11.7 m/s in October (corresponding to reduced thermal activity in late autumn).

Steppe Buzzard *Buteo buteo vulpinus*: Huge numbers of this highly migratory subspecies were observed in Israel under much better average thermal conditions than the nominate form in Europe. Gliding and flap-gliding speeds showed wide variation around 14.8/14.4 and 14.7/14.4 m/s, respectively. Spaar (1995) and Spaar and Bruderer (1997a) show the dependence of Steppe Buzzard migration on environmental conditions, particularly the correlation between climb rate in thermals and gliding speed. Even with sinking rates of less than 1 m/s Steppe Buzzards still flew faster on average (14 m/s) than the larger birds of the nominate form, and reached an average of 12.7/12.4 m/s in horizontal flight with a relatively high proportion of flapping. Mean cross-country speed was 9.9 m/s.

Long-legged Buzzard *Buteo rufinus*: Only gliding (14.9/14.6 m/s) and flap-gliding (15.0/14.8 m/s) birds were observed, providing air speeds similar to Steppe Buzzards flying under similar conditions.

Lesser Spotted Eagle *Aquila pomarina*: A wide variation of gliding and flap-gliding speeds averaging 15.0/14.5 m/s are typical for the migration of this species. Only rarely can flapping flight be observed; in the available two cases the average speed was 12.1/11.7 m/s in slightly descending flight. Average cross-country speed was 10.2 m/s.

Steppe Eagle *Aquila nipalensis*: Much bigger than *A. pomarina*, the Steppe Eagle has nearly the same mean and variation in air speed when gliding or flap-gliding (14.8/14.3 and 15.7/15.4). For a thorough discussion of flight speeds in relation to environmental conditions see Spaar and Bruderer (1996), for a comparison of various species: Spaar (1997). The air speed of one individual with four phases of flapping flight was only 7.9/7.7 km/h. Average cross-country speed was 9.7 m/s.

Imperial Eagle *Aquila heliaca*: The low air speed of 9.8/9.5 m/s of this species in mixed flight behaviour is based on a single individual in horizontal flight. During one interval, flapping more or less continuously, it accelerated to 10.4/10.2 m/s. On migration it flies at higher speeds, often with *A. pomarina* (Shirihai 1996).

Golden Eagle *Aquila chrysaetos*: Only gliding and flap-gliding speeds are available; the averages are in the same range as for other eagles (15.5/15.1 and 14.0/13.0 m/s). We consider this to be a reasonable value for cruising flight. Flapping flight is very rare; we expect its speed to be in the lower part of the measured range (comparable to *A. pomarina, nipalensis, heliaca* and *Hieraaetus pennatus*), while steeper glides may even exceed the speed of 22 m/s recorded in this sample.

Booted Eagle *Hieraaetus pennatus*: Gliding and flap-gliding speeds of this small species show wide variation and average 14.1/13.9 and 12.9/12.5 m/s, respectively. These speeds are similar to migrating buzzards and larger eagles under similar conditions. Mainly flapping individuals in horizontal flight flew at 11.5/11.3 m/s. Mean cross-country speed was 9 m/s.

Bonelli's Eagle *Hieraaetus fasciatus*: The average speed of two slightly ascending tracks of birds gliding in extended updrafts was 11.4/11.0 m/s, that of two descending tracks with mixed flight behaviour was 14.6/14.0 m/s.

Osprey *Pandion haliaetus*: The recorded flap-gliding (average 14.2/13.7 m/s) and gliding speeds (13.1/12.5 m/s) are realistic values for migration. Among the large species this has the most pronounced flapping flight (Bruderer & Jenni 1990); the speed of such continuous flapping flights averaged 12.1/11.4 m/s in our sample. Pennycuick (1997) reports a low value of 10.6 m/s in non-migratory flights at low level.

Lesser Kestrel *Falco naumanni*: Most individuals showed mixed flight behaviour at speeds varying around 11.6/11.3 m/s.

Kestrel *Falco tinnunculus*: The average of 12.7/12.3 m/s is slightly higher than in *F. naumanni*, to some extent possibly due to a higher sinking rate. One released individual demonstrated a typical flight speed in a situation of uncertainty (8.5/7.6 m/s). The air speeds of Kestrels in indoor flight experiments, varying around 8.3 m/s (Videler *et al.* 1988), support the idea that such low speeds are typical for energy saving flights under unnatural conditions. We think that our measurements of 168 flight phases (of 152 individuals) over 452 tracking minutes are reliable for economic flight. If we take only the data of 155 migrating birds from the Negev we get an average air speed of 13.2/12.9 m/s.

Red-footed Falcon *Falco vespertinus*: A mean of about

13.2/12.8 m/s and a range of 12 to 15 m/s compares well with the other falcons, considering the relatively high average sinking rate.

Hobby *Falco subbuteo*: Gliding speeds (17.8 m/s) were, due to high sinking rate, considerably higher than the normal flap-gliding speeds of 11.8/11.3 m/s. Maximum reliably measured diving speed is 30 m/s (Alerstam 1986).

Eleonora's Falcon *Falco eleonorae*: 12.9/12.8 m/s is a realistic value.

Sooty Falcon *Falco concolor*: The measured speeds are all very high, varying around 15.8/15.2 m/s at high average sinking rates.

Lanner Falcon *Falco biarmicus*: 11.7/11.1 m/s is lower than the speed of other large falcons in flap-gliding flight.

Peregrine Falcon *Falco peregrinus*: Most individuals showed the typical mixed flight behaviour of falcons with a wide range and an average of 12.5/12.1 m/s. Pennycuick *et al.* (1994) report average air speeds (considered by the authors to represent V_{mp}) in the same range for two tame Peregrines in horizontal flapping flight (11.8 and 13.7 m/s, respectively). One mainly gliding individual in our data reached 16.7 m/s. Alerstam (1986) measured 17.8 to 20.5 m/s in three birds vigorously flapping, while already descending in the initial phase of a stoop. Diving speeds along the slant flight path were in the range of 28 to 39 m/s (towards the end of 200 and 500 m dives, respectively). An even higher diving speed (51 m/s after a 334 m stoop) was measured by Peter and Kestenholz (1998).

Barbary Falcon *Falco pelegrinoides*: Two tracks of mainly gliding flights ($V_z = -1$ m/s) provided air speeds around 14.5/14.4 m/s. Highest diving speeds in relatively flat stoops reached 41.7 and 43.9 m/s after 173 and 189 m, respectively (Peter & Kestenholz 1998).

Chukar *Alectoris chukar*: The registered air speed of 14.8/14.2 m/s is realistic, and slightly higher than the speed mentioned by Norberg and Rayner (1991) for the smaller Grey Partridge *Perdix perdix*.

Crane *Grus grus*: Mean flap-gliding and gliding speeds between thermals over southern Israel were 14.8/14.6 m/s and 14.5/13.6 m/s. Alerstam (1975b) measured air speeds of 18.6 ± 2.5 m/s in active flight over the Baltic Sea.

Cream-coloured Courser *Cursorius cursor*: Four resident individuals in the Negev provided a realistic mean of 15.4/15.1 m/s.

Collared Pratincole *Glareola pratincola*: 12.5/12.1 m/s documented by eight tracks over fairly long distances are realistic and compare well with *G. nordmanni*.

Black-winged Pratincole *Glareola nordmanni*: Four tracks with five flight phases provide a realistic mean of 11.6/11.3 m/s.

Ringed Plover *Charadrius hiaticula*: A released bird provided a very low air speed of 10.6/10.6 m/s. Meinertzhagen's value of a small flock 'cruising on fore-shore' at 16.4 m/s seems to be more realistic for economic flights.

Lapwing *Vanellus vanellus*: The mean of 12.3/11.9 m/s seems realistic.

Dunlin *Calidris alpina*: Two released birds show a very low speed of 8.9/8.9 m/s. Noer (1979) provides two measurements at zero wind speeds (15.8 and 16.4 m/s) which are more realistic for distance flights; a speed of 14.4 ± 1.2 m/s is indicated for the Sanderling *C. alba*.

Ruff *Philomachus pugnax*: The observed air speed of 13.8/13.6 m/s is in the range indicated by Glutz von Blotzheim *et al.* (1975). Noer (1979) provides some good data for similar species: For the similarly sized Common Redshank *Tringa totanus* 15.5 m/s, for the smaller Red Knot *Calidris canutus* about 13.9 m/s (at zero wind speed), for the larger Oystercatcher *Haematopus ostralegus* 14.2 m/s without wind. Hedenström and Alerstam (1994) measured speeds of 13.9 m/s for Red Knots climbing at an average rate of 1.1 m/s.

Snipe *Gallinago gallinago*: The air speed of 16.0/15.5 m/s for an individual in horizontal flight seems realistic.

Curlew *Numenius arquata*: The two birds, both slightly climbing over short distances, had air speeds of 13.9/13.2 m/s in nearly windless conditions.

Green Sandpiper *Tringa ochropus*: The extremely high speed of free flying birds (23.1/22.7 m/s) is based on one track descending at a rate of 1.9 m/s, thus at the limit to be included in the present list. We will not use it for comparison with theoretical speed calculations, because it is well above the values of similar waders discussed under the Ruff. Interestingly, the speeds of two released birds ($V_z = -0.2$) were extremely low (5.8/5.8 m/s); they show the wide range of speeds which can be adopted by waders in spite of relatively high wing loading.

Common Sandpiper *Actitis hypoleucos*: Two releases provided typically low speeds (9.1/9.1 m/s at a climbing rate of 0.5 m/s).

Black-headed Gull *Larus ridibundus*: The air speed of 11.7/11.2 m/s is realistic. Schnell (1965) gives 10.1 m/s for the larger Ring-billed Gull *L. delawarensis*, while Tucker and Schmidt-Koenig (1971) report 12.6 m/s for the slightly smaller Laughing Gull *L. atricilla*.

The value provided by Pennycuick (1997) for the latter species is, as in other cases, very low, i.e. 9.5 m/s.

Common Gull *Larus canus*: The air speed of 11.6/11.1 m/s is nearly identical to the smaller *L. ridibundus*.

Lesser Black-backed Gull *Larus fuscus*: The measured mean air speed of 12.3/11.9 m/s of birds on migration is realistic in comparison with the other gull species. It is particularly close to the literature data of *L. argentatus* (see *L. cachinnans*). It may also be of interest that the speed of these migratory flights over the desert is lower than that of the sister species *L. cachinnans* on roosting flights.

Yellow-legged Gull *Larus cachinnans*: Mostly long-distance roosting flights at the southern tip of Mallorca show average air speeds of 14.3/14.0 m/s. This value may be above migratory speeds (see *L. fuscus*). For the Herring Gull *L. argentatus* Tucker and Schmidt-Koenig (1971) report 12.6 m/s, Schnell (1965) gives 11.2 m/s; Pennycuick's (1997) 9.9 m/s are at the lower end of the scale.

White-winged Black Tern *Chlidonias leucopterus*: The speed of 12.3/12.0 m/s is at the upper limit of the speeds (9.8–12 m/s) given by Gudmundsson *et al.* (1992) for the Arctic Tern *Sterna paradisea*. Among the radar data provided by Alerstam (1985) there are some of horizontally flying *Sterna paradisea* and *S. hirundo*, of which the average air speeds are between 10.5 and 15 m/s. Schnell (1965) measured 11.6 m/s for *S. hirundo*, but only 7.8 m/s for Black Terns *Chlidonias niger* above the breeding sites, which might correspond to the minimum power speed rather than cruising speed. Wakeling and Hodgson (1992) report air speeds of Common Terns of around 8.3 m/s for birds flying in crosswind or following wind, and an average of 12.2 m/s for birds flying against the wind. If speeds around 8 m/s are typical for leisurely flights, and speeds above 11 m/s are optimized flight speeds (such as against the wind), our average speed of 12.3/12.0 m/s seems realistic for migratory flights.

Crowned Sandgrouse *Pterocles coronatus*: The speed of 16.9/16.9 m/s is realistic compared to *P. orientalis* and *P. senegallus*.

Spotted Sandgrouse *Pterocles senegallus*: The air speed of 18.4/18.4 m/s fits well within the speeds of the other sandgrouse species.

Black-bellied Sandgrouse *Pterocles orientalis*: In slightly descending flight this is similar to *P. senegallus*: 18.9/18.3 m/s.

Rock Dove *Columba livia*: The measured speeds between 14 and 22 m/s (average 17.9/17.5) refer to wild Rock Doves in Israel. Wagner (1970) tracking homing pigeons by helicopter found speeds around 19 m/s for well-trained racing birds in Switzerland.

Woodpigeon *Columba palumbus*: Our speed data in the main range of 14 to 23 m/s (mean 18.1/17.6) for this heavy species compare well with the previous species and are not far from literature data: e.g. Alerstam and Ulfstrand 1974 (16.7 m/s), Norberg and Rayner 1991 (17 m/s).

Laughing Dove *Streptopelia senegalensis*: The single measurement of 12.4/11.5 m/s is realistic compared to the heavier *Columba* species. Evans and Drickamer (1994) give ground speeds of 9.9 ± 0.37 (day) and 12 ± 0.75 m/s (evening, likely to refer to roosting flights) for the Mourning Dove *Zenaida macroura*.

Cuckoo *Cuculus canorus*: The measured air speed of 11.0/10.4 m/s is based on only one released individual. The release effect may be responsible for this relatively low speed.

Short-eared Owl *Asio flammeus*: Three tracks of local birds at Malaga were all in the range of 7–9.4 m/s, resulting in the low average of 8.6/8.4 m/s.

Red-necked Nightjar *Caprimulgus ruficollis*: A single track of a local bird at Malaga indicates 9.0/8.9 m/s.

Alpine Swift *Apus/Tachymarptis melba*: The flight speed varied between 8 and 20 m/s. An average speed (V_{mr}) of 13.1/12.6 m/s seems realistic compared with smaller swifts.

Common Swift *Apus apus*: The flight speed is highly variable, depending on the actual behaviour. Bruderer and Weitnauer (1972) showed that speeds measured during roosting flights (likely to correspond to low values of V_{mp}) vary around 6.4 m/s, while migratory speeds (probably V_{mr}) vary around 11 m/s. The mean value of the present data (11.1/10.6 m/s) comprises about five times more (mainly migrating) individuals than the 1972 data set. Two released birds show only a slightly reduced speed (10.3/9.2 m/s). Oehme (1968) noted most speeds of diurnal flights in the range of 15–17 m/s, values which are in the same range as those reported by Bruderer and Weitnauer (1972) for hunting and display flights, but not for migratory flights.

Pallid Swift *Apus pallidus*: The mean air speed of 10.8/10.5 m/s is close to the other swifts; variation is probably only reduced due to lower number of tracked individuals under less varying conditions.

Bee-eater *Merops apiaster*: The birds were flying at speeds of 7 to 19 m/s, with an average of 12.5/12.2 m/s. 28 tracks and 105 minutes recording time are a reliable sample.

Hoopoe *Upupa epops*: A speed of 11.1/11.1 m/s is reasonable, but based on one individual only.

Woodlark *Lullula arborea*: 10.4/9.8 m/s is rather low and based on only one measurement.

Skylark *Alauda arvensis*: The air speed of 13.3/12.7 m/s is higher than our own measurements for the Starling, but lower than the average speed measured by Hedenström and Alerstam (1996) in migrating birds (15.4 m/s); they measured 6.5 m/s in songflights, which can be assumed to represent V_{mp}.

Sand Martin *Riparia riparia*: The mean flight speed of 11.7/11.3 m/s is the same as in other hirundine species. Schnell (1965) measured 9.4 m/s ground speed in weak winds near the colony and 13.7 m/s ground speed in variable winds while feeding.

Crag Martin *Ptyonoprogne/Hirundo rupestris*: The only measurement available indicates an air speed of 10.0/9.9 m/s, which is lower than that of the similar House Martin.

Barn Swallow *Hirundo rustica*: The air speed of 11.5/11.3 m/s compares well with other hirundines. Turner (1982) mentions 13.9, 10.4, and 6.9 m/s as fast, medium, and slow speeds of feeding birds. Blake *et al.* (1990) confirm the lower range indicated by Turner (1982) and measurements by Schnell (1965) for feeding flights: birds flying low (below 0.5 m) over the ground flew at average speeds of 8.6 m/s, birds above 0.5 m showed more erratic flights and averaged 6.8 m/s. Speeds of migratory flights are higher: L. Bruderer (1999), analysing radar tracks of birds arriving from Africa at the Andalusian coast, found speeds in a range of 10.5 to 18 m/s, if all birds (with an average sinking speed of –1.2 m/s) were included; if only birds with sinking rates above –0.5 (24 nearly horizontally flying birds) were included, the average speed was 12.8 m/s. In the windtunnel, the swallows started to drift backwards when the airflow was increased above the latter speed.

Red-rumped Swallow *Hirundo daurica*: Our recorded flight speed of 12.0/11.6 m/s is similar to *H. rustica*.

House Martin *Delichon urbica*: Air speeds were highly variable (6 to 18.5 m/s), but show a well documented average at 11.4/11.0 m/s. Bryant and Turner (1982) report 11.5 m/s for flights between feeding area and nest. L. Bruderer (1999), analysing radar tracks of birds arriving from Africa at the Andalusian coast, found speeds between 10.2 and 18 m/s, when all birds (with an average sinking speed of –0.8 m/s) were included; if only birds with sinking rates above –0.5 m/s (19 nearly horizontally flying birds) were included, the average speed was 12.9 m/s; in the windtunnel, the martins appeared to fly at their upper limit when the airflow approached this speed.

Tree Pipit *Anthus trivialis*: Four tracks of free flying birds provide a realistic average of 13.0/12.0 m/s. The very low speeds of eight released birds (varying around 7.5/7.0 m/s) demonstrate supremely the difference between release and free flight.

Meadow Pipit *Anthus pratensis*: Six tracks of free flying birds provided a relatively low average air speed of about 10.9/10.5 m/s. Four released birds provided typically low values around 9.4/8.8 m/s.

Yellow Wagtail *Motacilla flava*: Yellow Wagtails showed a particular flight behaviour when released at an Alpine pass. Some of them seemed to be highly motivated for migration and reached flight speeds (average 13.3/11.9 m/s) close to free flying individuals (13.3/12.7 m/s). Five of nine released birds, however, flew at very low speeds (6.7/6.1 m/s) similar to other released birds. The high speeds are close to that reported by Meinertzhagen (1955) for migrating flocks in Kenya (measured by theodolite). This is an excellent example of two well-separated speeds.

Pied Wagtail *Motacilla alba*: The mean of 13.6/13.0 m/s compares well with the Yellow Wagtail and the Tree Pipit.

Dunnock *Prunella modularis*: The average speed of seven released birds demonstrates clearly the release effect, resulting in low speeds varying around 8.4/8.0 m/s, while the only free flying individual provided a relatively high, but realistic migratory speed of 13.6/12.2 m/s.

Robin *Erithacus rubecula*: The observed speed of 8.1/7.5 m/s is very low, as usual in released birds. Stark (1996) reports air speeds ranging from 6 to 16 m/s and an average of 11.25 m/s for free flying nocturnal migrants (identified as Robins from wing-beat pattern and phenology). This is a realistic migratory speed. Individuals flying above 2000 m asl showed an average of 11.9 m/s according to Stark (1996).

Black Redstart *Phoenicurus ochruros*: The average speed of these released birds was 9.7/9.3 m/s, which is lower than the average migratory speed (11.1 m/s) of large samples of unidentified small nocturnal passerine migrants (Liechti & Bruderer 1995, Liechti 1992, Bruderer 1997b).

Redstart *Phoenicurus phoenicurus*: The very low speed of 8.0/7.5 m/s reflects a substantial release effect.

Whinchat *Saxicola rubetra*: The low air speed of 8.5/8.1 m/s reflects a substantial release effect.

Wheatear *Oenanthe oenanthe*: Two released individuals show a speed (14.3/13.1 m/s) close to the single free flying bird (13.4/12.8 m/s). The flight speed of the released birds is apparently not reduced by the unnatural situation as in other species. An air speed of 14 m/s is not unrealistic for cruising flight. It is, however, relatively high compared to the following larger species of the Turdinae.

Rock Thrush *Monticola saxatilis*: Only one individual observed over a very short time. The measured speed of 15.6/15.5 m/s is relatively high, though not unrealistic.

Blackbird *Turdus merula*: Our value of 9.8/9.3 m/s in non-migratory flights is very low; it is, however, confirmed by Oehme (1980) for flights in a park area. Glutz von Blotzheim and Bauer (1988) suggest realistic migratory speeds of 11 to 14.5 m/s. Most of the values listed by Meinertzhagen (1955) vary around 13 m/s.

Fieldfare *Turdus pilaris*: The speed of 13.0/12.4 m/s corresponds to that suggested as a realistic migratory speed for the Blackbird.

Song Thrush *Turdus philomelos*: The released birds seem to have made the transition to normal migratory flight; their air speed (12.65/11.9 m/s) is even slightly higher than the speed of eight free flying birds (12.25/11.7 m/s). Stark (1996) mainly measured air speeds in the range of 12.8–16.7 m/s (average of 51 birds = 14.6 m/s) in birds identified from wing-beat pattern and phenology in the Alps; he found no increase of speed with altitude. Alerstam (1975a) gives 12.8 m/s for migrating Redwings *Turdus iliacus*.

Mistle Thrush *Turdus viscivorus*: The speed of 12.65/12.4 m/s is lower than in the similarly sized *T. pilaris*; it is probably below normal migratory speed.

Marsh Warbler *Acrocephalus palustris*: Two releases provided a low average of 9.5/8.8 m/s.

Reed Warbler *Acrocephalus scirpaceus*: Releases in central Europe and in Malaga provided a low average speed of 6.7/6.6 m/s.

Great Reed Warbler *Acrocephalus arundinaceus*: One release provided a low value of 7.4/7.1 m/s.

Icterine Warbler *Hippolais icterina*: The air speed of 7.5/6.7 m/s is a reduced speed after release.

Melodious Warbler *Hippolais polyglotta*: A released bird flying extremely slow: 5.8/5.7 m/s.

Orphean Warbler *Sylvia hortensis*: One released bird flew at the very low speed of 6.6/6.6 m/s.

Lesser Whitethroat *Sylvia curruca*: Two released individuals with low speeds around 9.15/8.2 m/s.

Whitethroat *Sylvia communis*: These released birds reached realistic cruising speeds of 11.2/10.6 m/s.

Garden Warbler *Sylvia borin*: 9.8/9.2 m/s of these released birds was below expected cruising speed.

Blackcap *Sylvia atricapilla*: 8.7/8.2 m/s (released birds) is below the speed of small nocturnal passerine migrants (Liechti & Bruderer 1995, Liechti 1992, Bruderer 1997b).

Willow Warbler *Phylloscopus trochilus*: The observed speed of 10.0/9.5 m/s may be only slightly below cruising flight. Meinertzhagen (1955) gives 10.5 and 12 m/s

for birds chased by cars. See also *R. regulus* for comparison.

Goldcrest *Regulus regulus*: One released individual showed a low air speed of 6.6/6.0 m/s. Stark (1996) reports realistic values for migratory flights of *Regulus* sp. based on 57 individuals identified from wing-beat and phenology with a range of 5-12 m/s and an average of 9 m/s.

Firecrest *Regulus ignicapillus*: The observed speed of 7.4/6.7 m/s is slightly higher than in *R. regulus* but still lower than the average of migratory birds (9 m/s) reported by Stark (1996); a release effect cannot be excluded in our measurements.

Spotted Flycatcher *Muscicapa striata*: The speed of 14.6/13.4 m/s is very high compared to other releases; it may even be above normal cruising speed in still air due to prevailing head wind.

Pied Flycatcher *Ficedula hypoleuca*: The observed air speed of 10.7/9.5 m/s is relatively low, particularly compared with *Muscicapa striata*. Pied Flycatchers are good fliers when released, but the speed, which is well documented by 21 individuals during ten tracking minutes, seems nevertheless reduced by release effects.

Great Tit *Parus major*: Our only speed value of 14.0/13.6 m/s is high for such a small bird. Norberg and Rayner (1991) give a very low value of 8.1 m/s for the Blue Tit *P. caeruleus* with unknown source and conditions; this value was retained by Welham (1994).

Red-backed Shrike *Lanius collurio*: The mean value of our sample (14.1/12.9 m/s) is close to other reported values of released migrants and non-migrating individuals, respectively (Biebach *et al.* 1983, Jakober & Stauber 1987). We assume that cruising speeds are not much higher.

Jay *Garrulus glandarius*: An air speed of 13.5/12.9 m/s seems relatively high, but nevertheless reasonable.

Jackdaw *Corvus monedula*: A migratory speed of 15.4/14.7 m/s is high for this relatively small corvid. However, Glutz von Blotzheim and Bauer (1993) state that the species flies faster than *C. corone* and *C. frugilegus* under similar conditions.

Rook *Corvus frugilegus*: The mean air speed of 13.8/13.0 m/s on migration seems low, but is still higher than that of *C. corone* on roosting flights.

Carrion Crow *Corvus corone*: 10.5/9.9 m/s as an average air speed of birds on mainly roosting flights is rather low, but is confirmed by Oehme (1965) who reports values of 8.3 to 11.1 m/s. Glutz von Blotzheim and Bauer (1993) suggest 9.4–12.5 (up to 13.9) m/s as realistic values. For details of the variation in speeds see Althaus and Bruderer (1982). Tucker and Schmidt-Koenig (1971) measured 12.7 m/s for the American

Crow *C. brachyrhynchos.*

Brown-necked Raven *Corvus ruficollis*: The air speed of 14.7/14.3 m/s of this relatively small raven is higher than that of the preceding crows; it may support to a certain extent the high speed measurements in *C. corax.* However, the measurements are characterized by wide variation and an average vertical speed of –1.3 m/s. If vertical speed is restricted to values > –0.9 the remaining nine birds had an average speed of 12.8/12.4 m/s which is similar to the Rook.

Common Raven *Corvus corax*: The measured (non-migratory) speeds show wide variation around the very high mean of 15.3/14.1 m/s. This includes only horizontally flying and slightly descending birds. Steeply descending birds reached even higher speeds. This value is higher than the 12.5–13 m/s reported by Mauersberger (1980) and at the upper limit of those mentioned by Meinertzhagen (1955). We assume a lower speed than our measured average for economic cruising flight.

Common Starling *Sturnus vulgaris*: Our 12.9/12.4 m/s are lower than older measurements (Meinertzhagen 1955, Delvingt 1962), but similar to or higher than reported by recent radar studies (Schnell & Hellack 1978: 10.5 m/s; Evans & Drickamer 1994: 10.0 ±0.4 m/s in daytime and 12.7 ±0.9 m/s in roosting flights). Our measured speeds seem to be rather low for cruising flights, particularly when compared to the finches.

Chaffinch *Fringilla coelebs*: The mean air speed of 13.4/12.8 m/s is somewhat higher than the average value (12.3 m/s) drawn from Gatter (1979).

Brambling *Fringilla montifringilla*: The average speed of 12.2/11.6 m/s is somewhat lower than in the Chaffinch and lower than the realistic migratory speed of 13.5 m/s drawn from Gatter (1979).

European Serin *Serinus serinus*: The very low speed of 8.1/7.2 m/s is likely to be a consequence of the release.

European Greenfinch *Chloris chloris*: The observed air speed of 13.2/12.2 m/s compares well with other finches.

European Goldfinch *Carduelis carduelis*: The speed of 13.2/12.8 m/s is a typical finch speed.

Eurasian Siskin *Carduelis spinus*: Two individuals taking off showed a very low speed of 7.0/6.7 m/s, while two flocks of ten and 15 individuals, respectively, showed an average speed of 13.25/12.4 m/s. These measurements indicate two speeds or gaits under natural conditions.

Common Linnet *Carduelis cannabina*: The value (15.8/15.8 m/s) of one released bird is very high.

Common Redpoll *Carduelis flammea*: 9.5/8.4 m/s (only one released individual) is likely to show a release speed rather than migratory speed.

Ortolan Bunting *Emberiza hortulana*: The low observed air speed (8.7/7.7 m/s) is explained by the release effect and a climb rate of 2 m/s. It is considerably below the speedometer measurements of normally-flying Yellowhammers *E. citrinella* given by Meinertzhagen (1955) which are between 9.7 and 13.3 m/s.

MEASURED SPEEDS AND MODELS OF OPTIMAL FLIGHT SPEED

Theoretical predictions

Predictions about air speeds of birds are made by means of the U-shaped power curve which is a plot of power P against velocity V. Two characteristic speeds of this curve can easily be defined. V_{mp} is the speed of minimum power, which minimizes energy cost per unit time and is used simply to remain airborne (such as in nocturnal flights of Swifts, Bruderer & Weitnauer 1972, and in song flights of Skylarks, Hedenström & Alerstam 1996), in large birds which are limited to low-cost flights by their size, or in birds in an uncertain situation (e.g. when released after being captured). V_{mr} is the speed of maximum range and minimizes the energy cost per unit distance covered; it is found by drawing a tangent from the zero point to the power curve and is used by birds maximizing distance flown in a migratory flight with a certain amount of fuel (Pennycuick 1975, 1989). Alerstam and Lindström (1990) and Alerstam (1991) drew attention to the possibility that migrants might tend to minimize the total duration of the migratory journey – incorporating time for flight and intervening periods of fuel storage. This third speed $V_{opt} = V_{mt}$ (speed of minimum time), which exceeds V_{mr} by a variable amount, might be used by birds whose objective is to maximize the overall speed of migration. This speed is less well defined than V_{mp} and V_{mr}, but was used to explain why many small birds migrate faster than the predicted V_{mr} (Welham 1994). Generally, the difference between V_{mr} and V_{mt} is quite small (Hedenström 1993). Flight speeds close to a species' or individual's upper power limit will be used when energy optimization has low priority (e.g. when escaping a predator).

V_{mr} is expected to vary with wind, and with mass changes due to varying fuel reserves (Pennycuick 1978, Liechti *et al.* 1994); the same holds for V_{mt}. V_{mr} and V_{mp} will increase with fuel load. All characteristic flight

speeds (V_{mp}, V_{mr}, V_{mt}) should increase with increasing altitude due to reduced air density (Hedenström & Alerstam 1995). Variation of air speed with wind is well documented by field measurements (Bellrose 1967, Bruderer 1971, Bloch *et al.* 1981, Liechti 1992). Speed increments with altitude are shown by some field data (Bruderer 1971), but not consistently for different species (Stark 1996). In the data set presented here these effects are part of the wide variation. To get an idea of the potential effect of air density on speed we provided the equivalent air speed at sea level (EqV_a) in the lists and in the species account.

For gliding birds (dynamic soaring or between thermals), performance can be analysed in a manner analogous to that for flapping flight, using the relationship between rate of sink and forward gliding speed to predict optimal speeds under various conditions (Pennycuick 1975, 1989, Alerstam 1991). Studies on soaring migrants in Israel proved that raptors from the size of Marsh Harriers upwards maximize cross-country speed by adjusting gliding speed to the actual climbing rate in thermals (Spaar 1996, 1997, Spaar & Bruderer 1996, 1997a, 1997b). This variation is included in the present data as far as gliding and flap-gliding individuals are considered, while it is excluded in horizontal flapping flight of soaring birds.

Welham (1994) compared literature reports of speeds of 48 avian species (supposed to be on migration) with the predictions of V_{mr} derived from three aerodynamic equations (Greenwalt 1975, Pennycuick 1975, 1989, Tucker 1974, 1975). While species between 0.1 (or 0.3) kg and 3 kg appeared to migrate at V_{mr}, lighter species almost always flew faster than V_{mr}, whereas heavier species showed the opposite trend.

Recently Pennycuick (1997), reassessing his calculations of 'optimum' flight speeds, compared two versions of calculating V_{mp} with non-migratory speeds (measured at low levels over relatively short distances by ornithodolite) of 36 mainly medium-sized and large birds. Our species accounts show that Pennycuick's measurements are consistently lower than our values and those of other authors. Assuming that these low speeds were minimum power speeds, Pennycuick found that they were still higher than the estimated V_{mp}. As he found the same discrepancy in two birds of differing sizes flying in a wind tunnel (Pennycuick *et al.* 1996), he corrected for this discrepancy by replacing the previously used default values for the body drag coefficient C_{Db} from 0.25 (in large birds) and 0.40 (in small birds) to 0.1 (for all birds), assuming that for well streamlined birds the true value may be as low as 0.05 and above 0.1 for others (Pennycuick 1997). By decreasing the value of C_{Db} the predicted speeds (V_{mp} as well as V_{mr}) are increased, thus the quotient of observed air speed over calculated V_{mp} was pushed downward to equal 1 on average. By using the same C_{Db} for large and small birds, all speeds are increased, but those of small birds slightly less than those of large birds.

Pennycuick (1997) emphasizes that current ideas about time or energy minimizing migratory flights (Alerstam & Lindström 1990 and Hedenström & Alerstam 1995) assume that the birds are able to choose between various optimal speeds. Revising these assumptions, he concludes that 'flying at the maximum range speed on migration may not represent an optimal or even a practical strategy and that cruising speed may be limited by the muscle power available or by aerobic capacity'. His conclusion is particularly astonishing, when considering the high predictive value of his older models, e.g. with respect to V_{mr} and V_{mp} in Common Swifts on migratory and roosting flights (Bruderer & Weitnauer 1972), or in Skylarks on migratory and song flights (Hedenström & Alerstam 1996), or with respect to the adjustment of V_{mr} to tail and head winds (Bellrose 1967, Bruderer 1971, Liechti 1992, Liechti *et al.* 1994), or with respect to optimization of the gliding speeds by soaring birds according to lift in thermals (Spaar 1996, 1997, Spaar & Bruderer 1996, 1997a, 1997b).

The basis for comparison

Our comparisons consider the allometric formulae of Rayner (1995) and the model suggested by Pennycuick, applying the two different default values for the drag coefficient (Pennycuick 1992, 1996). First we check for the relationship between the equivalent air speeds of free flying birds from Table 3 and the mass of birds according to Table 1, because flight speed is assumed to increase with body mass, larger birds being forced to fly faster in order to generate sufficient lift on their wings (Norberg & Rayner 1991). Then we compare the equivalent air speeds from Table 3 with calculated V_{mr} and V_{mp}, based on morphological values from Table 1 and the default values given by Pennycuick (1992, 1996). Calculated V_{mp} is additionally compared with so-called 'minimum speeds', comprising the released birds, the minimum speeds of all other flapping fliers and the pure flapping flights of soaring migrants (assuming that they may be close to V_{mp}). As most data are derived from migratory flights, even the lowest recorded speeds of many, particularly small species will be above V_{mp}.

Speed and body mass

In our data, air speed correlates non-significantly with mass at a rate of only $M^{0.02}$ (Fig. 1). This deviates considerably from the factor of $M^{0.14}$ suggested by Rayner (1995). Passerines and falcons show no within-group increase of speed with size (Fig. 1); the same is true for herons (Table 3) and for soaring migrants in powered flight (Fig. 1).

Measured speeds and predictions of aerodynamic models

Measured air speeds (reduced to sea level, Table 3) were compared with the models of Pennycuick (1992, 1996) and Rayner (1995) by dividing EqV_a by predicted V_{mr} or V_{mp} and plotting the quotients against the mass of the birds (Figs 2, 3 & 4). The horizontal line at quotient 1.0 indicates perfect agreement. All figures show a negative correlation between the quotients and mass.

In the case of Pennycuick (1992) (with C_{Db} between 0.25 and 0.40), equivalent air speeds EqV_a of medium sized birds are close to predicted V_{mr}, while those of small birds are above, those of large birds below prediction (Fig. 2a). The quotients resulting from Pennycuick's (1996) suggestion ($C_{Db} = 0.1$) are all below the line of complete agreement; the decrease with mass is, however, slightly reduced in comparison with the 1992 version (Fig. 2b) due to the same C_{Db}-value being used for large and small birds.

Figure 3 compares EqV_a based on measured air speeds (Table 3) with V_{mp} calculated according to

Pennycuick (1992). The equivalent air speeds of small birds are higher than predicted V_{mp} by a factor of about 2.3; for medium-sized birds the factor is roughly 1.6; in large birds the measured values tend to approach the calculated values. If only so-called 'minimum speeds' are used for the comparison (Fig. 3b), the speeds of most released birds are still higher than predicted V_{mp}, but only by a factor of about 1.5; flapping soarers approach predicted V_{mp} with increasing size. The scatter of measured minimum speeds is enormous, because for many species no measurements of individuals in slow flight are available; 'minimum speeds' of large birds are, however, scattered around predicted V_{mp}.

Dividing average recorded air speeds EqV_a by V_{mr} calculated according to Rayner (1995) (Fig. 4) shows a result which closely matches that of Figure 3a, indicating that Rayner's formula for V_{mr} provides predictions close to Pennycuick's (1992) model for V_{mp}, but has not much to do with Pennycuick's (1992) predictions of V_{mr} (Fig. 2).

DISCUSSION

Measurements and presentation

This paper presents air speed data of 139 western Palearctic bird species. High reliability of the data is given by the fact that all the data are recorded by the same high precision tracking radar (Bruderer *et al.* 1995) and by frequent on-site wind-measurements at the flight levels of the birds.

The large number of species and measurements available allowed us to present the data graphically,
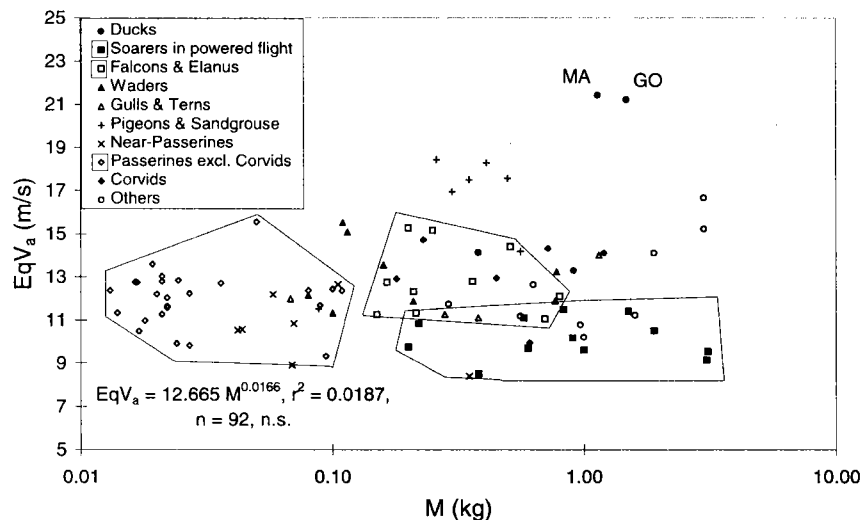
Figure 1. Mean equivalent air speed at sea level EqV_a of free-flying birds in flapping flight (only powered flight for soarers) measured by radar vs. average species body mass M. GO, Goosander; MA, Mallard.

2a

2b
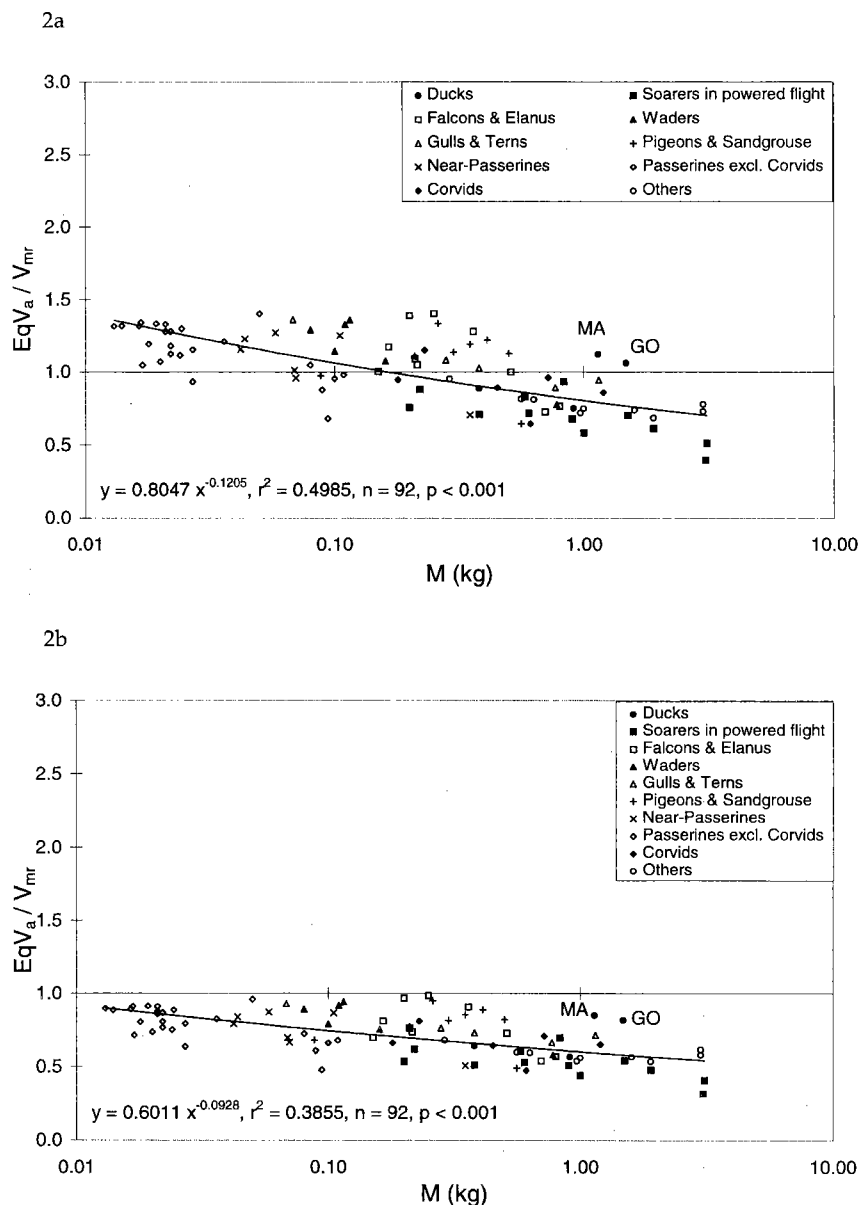
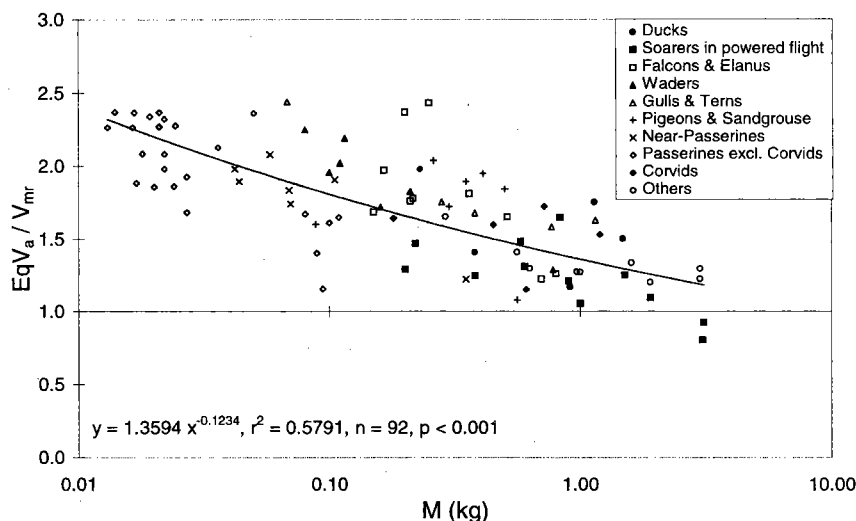**Figure 2.** Mean equivalent air speed at sea level EqV_a of free-flying birds in flapping flight (only powered flight for soarers) measured by radar divided by species-specific speed of maximum range V_{mr} calculated with two versions of programme 1, Pennycuick (1989) vs. average species body mass M. GO, Goosander; MA, Mallard. (a) version 1.1, 1992; (b) version 2.0, 1996.

emphasizing natural variation instead of mean values, and allowing easy interspecific comparison. Variation is increased by environmental conditions and by including tracks with vertical speeds of up to ± 2 m/s. We included vertical speeds beyond ± 0.5 m/s to provide data for as many species as possible, but clearly stated if a bias should be expected due to ascent or descent. For biological interpretation, it is important to show variation and to indicate: (a) the average vertical speeds, (b) the variation of ground speeds and

(c) to calculate EqV_a because of different altitudes at which the tracks were recorded. Unlike many speeds reported without details in the literature, often based on single incidental measurements, we emphasize details of single species or samples, as well as problems of some measurements in the 'species accounts'.

In our sample, birds with high wing-loading (water-birds/waders) and species with large aspect ratios (particularly seabirds) are under-represented. In con-

3a

3b
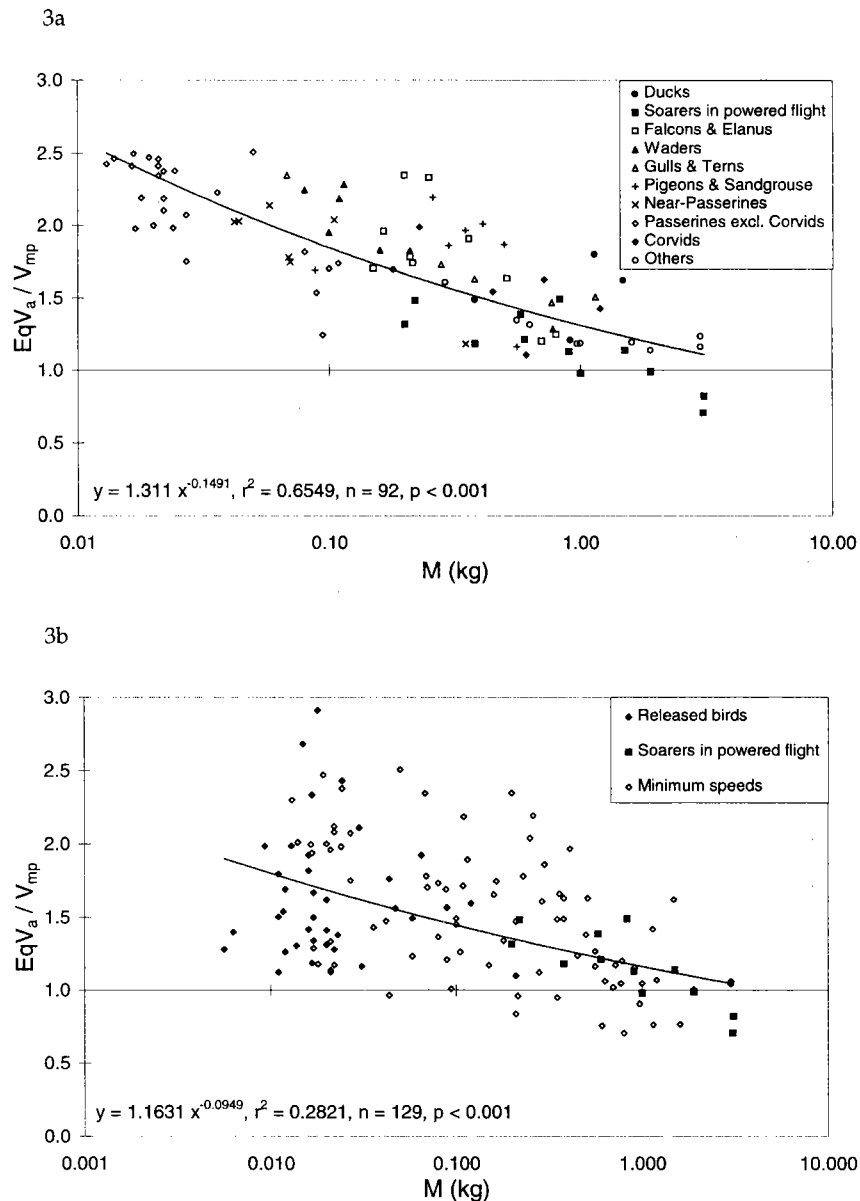
Figure 3. Mean equivalent air speed at sea level Eq V_a of birds measured by radar divided by species-specific speed of minimum power V_{mp} (calculated with programme 1, version 1.1, Pennycuick 1992) vs. average species body mass M. (a) Free-flying birds in flapping flight and powered flight for soarers; (b) released birds, and minimum speeds of other free flying birds and soarers in powered flight.

trast, Pennycuick's (1997) sample comprises mainly medium to large birds with high wing-loadings or high aspect ratios. The difference is even more pronounced in the sample given by Spear and Ainley (1997). Welham (1994), dealing with data from various sources, was able to select for a more balanced collection of flapping species, but avoiding soaring landbirds completely and including only two dynamically soaring seabirds.

Variation around two typical speeds

As many nocturnal migrants could not be identified to the species in natural migratory flights, released birds had to be included in the data set. As their behaviour does not correspond with normal flight, they are specially identified in Table 3. These release flights led to the empirical confirmation of a very low speed utilized by individuals in a state of uncertainty. Such low flight

Figure 4. Mean equivalent air speed at sea level $Eq V_a$ of free-flying birds in flapping flight (powered flight for soarers) measured by radar divided by species-specific speed of maximum range V_{mr} calculated according to Rayner (1995) vs. average species body mass M.

speeds are also reported by Emlen and Demong (1978) where White-throated Sparrows *Zonotrichia albicollis* were experimentally released high above ground and showed air speeds close to expected V_{mr} under clear sky, but speeds close to expected V_{mp} when released under overcast sky. Table 3 shows that passerines and near-passerines in normal migratory flights prefer air speeds in the range of 10 to 15 m/s (40 to 55 km/h), while most released birds are within the range of 5 to 10 m/s (20 to 40 km/h). The difference is also clearly documented for waders and one falcon. This is convincing evidence that birds choose different flight speeds for different purposes. The theoretical speeds of minimum power and maximum range are the obvious candidates to explain the two speeds. This agrees with most publications by Pennycuick (1969, 1975, 1989, 1995) and others (Greenewalt 1975, Rayner 1990, 1995) but not with Pennycuick's (1997) reassessment of flight speeds, where he questions such a selection for specific speeds. Our data prove that birds have the capability of flying at different speeds, and that certain 'gaits' (Rayner 1988, 1995) may be chosen according to circumstances, the lower gait suggesting something like V_{mp}, the higher indicating an optimized speed for migration, which may correspond to V_{mr} and according to Pennycuick (1969, 1989, 1992) nearly doubles V_{mp}.

The wide variation in our samples and the partial overlap of the two speed gaits suggest that power margins around the optimal speeds are much wider in small birds than expected or that the power curve may be less steep than commonly assumed. It does not

seem to cost the smaller birds too much to vary their speed over 3–5 m/s which may be 40–70% of the speed of minimum power and 25–40% of the speed of maximum range. In spite of two obvious speed ranges, at least small birds seem to be capable of selecting a wide range of speeds around the two optima. This results in something like a continuum of available speeds, a possibility which was questioned by Rayner (1995) in view of potential constraints due to the mechanical properties of muscles. Our data support (at least for small birds) a conclusion drawn by Schnell and Hellack (1979) on the basis of a much smaller dataset, stating that '.....air speeds can be increased or decreased considerably with only relatively small increase in metabolic rate or cost of transport'.

Such a continuum of speeds was demonstrated for *Hirundo rustica* and *Delichon urbica* in free flight as well as in a windtunnel, where both species controlled speed by varying the proportion of partial bounding (Bruderer, L. 1999). Other small passerines seem to achieve this flexibility mainly by full bounding, i.e. by closing the wings completely during the pausing phases in their wingbeat pattern. During bounding profile drag is reduced to zero during a fraction of time which corresponds to the proportion of pausing phases. This proportion often comprises 25–75% of the flight time (Bruderer 1971). Thus, in simplified model calculations, profile drag should be reduced to zero for about half of the flight time (neglecting the obviously wide variation induced by the flight type of the species involved, the flight phase, and environmental condi-

tions). Larger passerines like Starlings (Tobalske 1995) and some thrushes (Stark 1996) as well as hirundines (Bruderer, L. 1999) achieve drag reduction combined with residual lift, by partial bounding. During a variable time between single wingbeats (hirundines) or bursts of wingbeats (thrushes, starlings) they fold their wings to an arrow-like shape, keeping the arm-wing open as a residual airfoil (partial bounding), thus avoiding too much sinking during the pausing phases, but still achieving higher speeds than assumed by conventional model calculations.

Deviations from model predictions

Mass-relationship is negligible in our sample. On the other hand, there are important group-specific deviations (e.g. some nocturnal birds with very low speeds; pigeons, sandgrouse and some waterbirds with very high speeds). The result of allometric comparisons will, therefore, depend heavily on the species included (Rayner 1988).

However, in spite of the fact that our sample is biased towards passerines, including relatively few birds with high wing-loadings or aspect ratios, it shows a similar difference to Pennycuick's (1992) model as the sample of Welham (1994). Welham (1994) tried to explain the underestimation of speeds in small birds by assuming time-minimizing, and therefore increased migratory speeds, as suggested by Alerstam and Lindström (1990) and Lindström and Alerstam (1992). For the overestimation of speeds in large birds he assumed an increasing limitation of sustained power output with size, as suggested by Pennycuick (1969, 1975).

Our data support the view that there are important speed limitations in large birds. It seems that available power output for flight declines even faster with size than previously assumed. The limitation even leads to constant speeds within the whole size range of herons in our sample. A similar limitation applies when horizontal flapping flight is considered for soaring birds. Predictions of speeds for large birds will have to pay more attention to such limitations in future.

V_{mr} calculated according to Pennycuick (1992 and earlier) produces reasonable predictions for the speeds of medium-sized birds (such as crows, gulls, terns, waders and small raptors). Predictions for small birds which do not usually close their wings during pausing phases (such as swifts, swallows, starlings and some thrushes using partial bounding or flap-gliding flight) may also come relatively close to reality. The main discrepancy between model and measurements appears in

small birds using bounding flight. By closing their wings during the passive phase of the wing-beat cycle they reduce profile drag to zero, while proceeding on a ballistic trajectory. Tobalske and Dial (1994) showed that Budgerigars *Melopsittacus undulatus* flying in a windtunnel tended to shift from flap-gliding at low speed to flap-bounding at high speed. Similarly, Tobalske (1995) observed that Common Starlings tended to use flap-gliding at low speeds, partial bounding at intermediate speeds and flap-bounding in fast flights. It is evident that bounding flight is the flight mode that enables small birds to reach high speeds. These speeds are obviously higher than predicted by any aerodynamic model, because the ballistic phase is not appropriately accounted for. This explanation is more realistic than assuming that birds on migration would decide between V_{mr} and V_{mt} as suggested by Alerstam and Lindström (1990), Hedenström and Alerstam (1995) and Welham (1994). Pennycuick (1997) has already questioned this explanation. However, our data do not support his conclusion, that most birds would fly at V_{mp} instead of V_{mr}. Our data show that there are large speed differences between (a) birds likely to fly at speeds around V_{mp} (large birds and released small birds) and (b) the majority of small and medium-sized flapping-fliers using higher speeds (probably around V_{mr}) during normal migratory or roosting flights. The prediction of V_{mp} produced by Pennycuick's model (1992 and 1997) is far below our measured air speeds (Fig. 3a) even if the speeds included are restricted to released birds and lowest speeds of other flapping fliers (Fig. 3b); only birds above 1 kg are approaching the predicted V_{mp}. The prediction is much better when the measured air speeds are compared with predicted V_{mr}; for medium sized birds the agreement is optimal, when using the 1992 C_{Db} values (Fig. 2a). If using the new C_{Db} values (Pennycuick 1996, 1997; Fig. 2b) predicted V_{mr} is too high, approaching real speeds only in very small birds.

We suggest that reduced profile drag in bounding flight is the real explanation of the discrepancy between predicted and measured speeds of small birds and that the aerodynamic models have to be corrected in order to account for this ability of small birds to increase their speeds by reducing profile drag.

Conclusion

The aerodynamic model of Pennycuick (Version I, 1992) is still the best available for birds, but it should be adjusted to account for reduced profile drag in bounding flight and for speed limitations in large birds.

V_{mr} is the optimal speed for any flight in which a distance has to be covered economically. Field data confirm that such relatively high speeds are used for most flights and that during migration flight speeds are adjusted to wind and partially also to altitude according to theory. Speeds close to V_{mp} (which is much lower than V_{mr} in small birds) are used by: (1) birds which simply tend to remain airborne, e.g. roosting flights of Common Swifts or song-flights of Skylarks, (2) large birds approaching their limit of power output, or (3) birds in a state of uncertainty such as after being released.

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