

Wing area, wing growth and wing loading of Common Sandpipers *Actitis hypoleucos*

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This study investigates the changes in wing length, area and loading in Common Sandpipers as chicks grow, and as adults add extra mass (during egg-laying or before migration). Common Sandpiper chicks weigh about 17 g and have “hands” that are about 35 mm long at one week old, when the primaries are just emerging from their sheaths. They grow steadily to reach about 40 g, with hands about 85 mm long, at 19 days, when they are just about fledging. Their wings have roughly adult chord width at this age (~53 mm), but they continue to gain primary length (but not much mass) for a week or more, so that wing loading remains at about the same value as in (lean) adults, ~0.32 g/cm². However, masses increase substantially during egg-laying and as fat accumulates for migration, leading to a 90% increase in wing loading. This may explain the observed reluctance of females to fly during egg-laying. Birds accumulating fat seem more willing to fly; moreover studies on other waders suggest that flight muscle mass increases as the time for migration approaches while other organs shrink, so minimising the potential imbalance between wing loading and power available.

INTRODUCTION

Common Sandpipers have been studied in the Peak District of central England since 1977 (Dougall *et al.* 2010). Adults have been caught in single-shelf mist nets set, usually at dusk, across the narrow rivers along which they hold their territories. Since 1990, they have also been caught while feeding along the shore-lines of nearby reservoirs using various traps. Chicks have been caught by hand and ringed, sometimes being recaptured later either by hand or, after fledging, in the same mist nets and traps. From direct observation, it is evident that females during egg-laying are reluctant to fly, and not very manoeuvrable. The fledging period of Common Sandpipers is 26–28 days, but chicks can flutter off the ground by day 15 (Cramp & Simmons 1983), and can usually fly strongly by 19 days (pers. obs.). Therefore there is a period of about 12 days during which chicks gradually gain the ability to fly. During this time they are reluctant to fly, and often fly only a short distance and then run to hide. These observations have prompted this study. The questions I address are: what is the pattern of growth of the wings in Common Sandpipers, and how do wing shape and wing-loading change?

TERMINOLOGY

There are terminological problems with this sort of study. As Pennycuik (2008) remarks, the measurements typically made by ornithologists in the field do not include some of the critical data needed to understand aerodynamic performance. What is conventionally termed “wing length” by ornithologists is, aerodynamically, nothing of the sort. Wing length should either be half wingspan, or (less easy to measure) length from shoulder to wing tip. “Hand length” is a more

accurate description, and used here: it has been taken in the standard way (carpus to wing tip, using a stopped rule). “Maximum chord”, used in some terminologies as an alternative to “wing length”, is no more a measure of chord than of wing length; chord is the “width” of the wing in flight, from the front of the carpus to the tip of the third or fourth secondary behind it. Mass is the one useful datum routinely obtained, but ornithologists do not usually measure wingspan or wing area, both critical data. This attempt to assess the growth of Common Sandpiper wings also tries to relate the routine data to the useful ones.

A “wing planform” is a 1:1 drawing of the outline of a bird from above or below with its wings fully extended; “wing area” is the area of both wings and the bird’s body between the wing roots as taken from a wing planform or derived as described below.

METHODS AND MATERIAL

Data on hand length, mass and age were taken from ringing data collected in the Peak District of central England during 1989–2011 for 104 chicks at various ages from around 7 to 19 days. Age was sometimes known directly from hatching date; for other chicks, up to a bill length of 20 mm, age was estimated using an equation relating age to bill length (Holland & Yalden 1991a). Data collected during Apr–Jul 1989–2011 from the same breeding area are also used for a further 40 fledged young of known age, ranging from just fledged to fully grown and up to 14 days post-fledging, and for 92 adult males, 107 adult females and 80 fledglings of uncertain age. Birds were individually colour-ringed, so sexes were determined by observation of their courtship, the increased weight of egg-laying females, and their relative sizes when both birds of a pair were caught.

Wing planforms were drawn around 6 adult corpses, and wingspan (wing-tip to wing-tip) was measured on another 4 live adults. Wing chord was also taken from these drawings. Four of the corpses resulted from ringing accidents, in 1985, 1991, 1992 and 2010 (two drowned, one hit a rock, one was garroted by his mate following him into the mist-net). While regrettable, this is about 1.7% of the 232 individual adults mist-netted along the river for colour-ringing during 1977–2011 (numerous recaptures of adults and captures of fledglings are extra handlings, so the casualty rate per handling is much less than 1.7%) and this paper is an attempt to turn the mortality from a waste to a useful outcome. The planforms of 3 nearly or just fledged chicks were also drawn, from live birds in the field, to assess the changes in wing shape and proportion between fledging and adulthood. Pennycuik (1989) advocates measuring the area of traced planforms using graph paper, and this method was used here. However, it is relatively difficult to trace wing outlines but much easier to measure hand length and wing chord. An alternative method of estimating wing area from hand length and chord was therefore investigated, assuming that the hand wing approximated an isosceles triangle and the centre section a rectangle.

RESULTS

The hand lengths of breeding males averaged 110.4 mm ($n = 92$, $SD = 2.89$, range 103–119 mm), and those of females 114.4 mm ($n = 107$, $SD = 2.67$, range 107–120). Male wingspans averaged 352 mm (range 338–360, $n = 4$) and females

361 mm (range 360–362, $n = 4$). Hand length, more easily measured than wingspan, is therefore 32.1% of wingspan ($n = 9$, $SD = 0.34\%$, range 31.6–33.3%) with no difference between the sexes. The mean hand length for all adults (mean of male and female means), at 112.4 mm, is essentially the same as reported for migrants passing through the Gulf of Gdansk (112.2 mm; Meissner 1997) and through Ottenby (113.3 mm; Iwajomo & Hedenström 2011).

The mass of 92 males averaged 50.1 g ($SD = 4.8$, range 42.0–77.5 g); three of these, late in the season (6–21 Jul), weighed >60 g, and were obviously fattening for migration. Excluding these three, the mean was 49.6 g (range 42–58, $SD = 3.5$). Females showed a greater range, 50–91 g, inflated mostly by egg-laying birds in late April, May and early June, as well as a few impending migrants; whereas only three males weighed >60 g, 55 females did. It has been suggested previously (Holland *et al.* 1982) that females over 62 g be considered ovigerous, and discounted from estimating average masses. That leaves 64 females in this sample, with an average mass of 56.6 g ($SD = 3.1$, range 50–62 g) (Table 1). These averages match closely those already reported for Common Sandpipers breeding in the same study area (Holland *et al.* 1982) and in Norway (Løfaldli 1980) (Table 2).

Wing buds on young chicks include hand buds about 20 mm long. Initially, as they grow with the primaries still in pin and extended by fluffy chick down, a useful measurement is not possible. The smallest measurable wing, on a 7 day-old chick, had a hand length of 30 mm, but others of this age ranged from 34 to 36 mm (Table 3). These chicks weighed

Table 1. Measurements of Common Sandpipers *Actitis hypoleucos* caught during the breeding season in the Peak District, England. These data exclude males that weighed >60 g and females that weighed >62 g (see text). Fledglings were artificially divided into younger and older classes at a hand length of 103 mm, the length of the smallest male.

Age/sex	Mass (g) mean (range; N)	Hand length (mm) mean (range; N)	Wingspan (mm) mean (range; N)
Adult males	49.6 (43–58; 89)	110.8 (103–119; 92)	352 (338–360; 4)
Adult females	56.6 (50–62; 64)	114.4 (107–120; 107)	361 (360–362; 4)
Young fledglings	41.9 (42–47; 12)	96.3 (89–102; 12)	297 (291–300; 3)
Old fledglings	47.6 (39–54.5; 68)	110.0 (103–119; 68)	

Table 2. Hand length and mass of Common Sandpipers *Actitis hypoleucos*, comparing this and previous studies.

Age/sex	Mass (g) mean (range)	Hand length (mm) mean (range)	N	Location	Source
Adult male	?	108.7 (102–114)	13	Norway	Løfaldli (1980)
	51.6	111.5 (105–117)	24	English Peak District	Holland <i>et al.</i> (1982)
	49.0 (43–54)	110.8 (103–116)	92	English Peak District	This study
Adult female	?	115.3 (110–120)	19	Norway	Løfaldli (1980)
	57.5	115.7 (111–121)	16	English Peak District	Holland <i>et al.</i> (1982)
	54.8 (50–59)	115.1 (111–120)	119	English Peak District	This study

Table 3. The increase of mass and hand length in Common Sandpiper *Actitis hypoleucos* chicks and fledglings with age. Age was either known from hatching date and subsequent recapture, or estimated from bill length.

Age (days)	Bill length (mm)	Hand length (mm) mean (range, SD)	Mass (g) mean (range, SD)	N
6–10	13–15.5	38.3 (30–50, 7.7)	20.4 (16–27.5, 3.25)	12
11–12	16–18	54.3 (38–70, 8.8)	26.3 (21.5–31, 2.51)	17
13	15–17.5	55.4 (49–66, 5.0)	26.9 (24–31, 2.33)	20
14–15	17.5–19	66.7 (55–83, 8.9)	32.3 (28–36, 2.52)	17
16–17	19–22	73.3 (61–100, 9.6)	34.0 (27.5–43.5, 3.30)	21
18–19	20–23	84.8 (73–107, 9.5)	37.9 (34–45.5, 3.85)	13
20–33	21–26	100.2 (82–114, 9.3)	42.6 (36–49, 3.56)	40

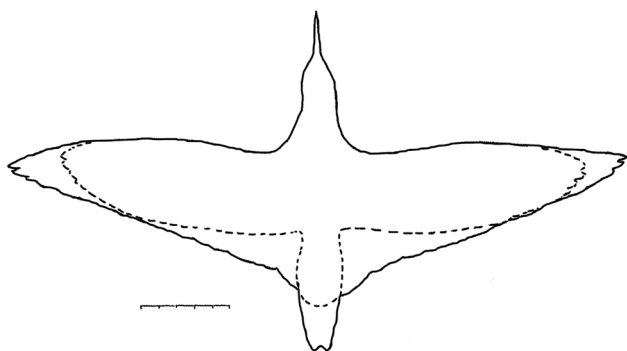


Fig. 1. Wing planform of an adult Common Sandpiper (solid line), with the outline of a just-fledged juvenile (dashed line). The wing tips of the young bird are much rounder, and the body is much shorter.

17–21 g. At 13 days, chicks had hand lengths of 49–66 mm, and weighed 24–31 g. By 15 days, they were 55–83 mm and 28–36 g, respectively. The lightest fledged bird, at 36 g, had a hand length of 90 mm, but the shortest wing of a fledgling was 83 mm and it weighed 41 g. Over a sample of 18–19 day-old birds, mean hand length was 84.8 mm (SD = 9.5, n = 13) and mass was 37.9 g (SD = 3.8, n = 13). Some of these had certainly just fledged, but others might still have been flightless; Common Sandpipers of this age sometimes run and hide, sometimes just fly a short distance and hide.

The minimum hand length recorded for an adult (male) bird in this study was 103 mm. If the un-aged fledglings are divided into those below and above this adult threshold, the younger ones had hand lengths of 96.3 mm (SD = 5.3, range 89–102, n = 12), while the older ones had hand lengths of 110.0 mm (SD = 4.66, range 103–119, n = 68). Thus the range of hand lengths was as extensive as that of the adults, and their mean is close to the mean of adult hand lengths (both sexes). Masses for the younger group were 42–47 g (mean = 43.5, SD = 2.4, n = 12), while the older birds had a range of 39–69.5 g (mean = 48.4 g, SD = 5.4, n = 68), including four exceptional birds, clearly already fattening for migration, at 61.5–69.5 g, on 8–28 Jul.

The wing areas of the adults were initially estimated as though each hand were an isosceles triangle, $\frac{1}{2}$ hand length \times chord. This simplifies to hand length \times chord for both hands combined. The area of the centre section was estimated as a rectangle, chord \times (wingspan $- 2 \times$ hand length). (By aerodynamic convention, the area of the body strip between the two wings is always included in the estimate of wing area; the air flow hitting the body is diverted over the wings so contributes to lift.) As Fig. 1 shows, these give a plausible approximation

to adult wing shape. However, the wing areas as estimated directly from the tracings were larger (calculated wing areas were between 82 and 92% of the directly measured figures), so are used here (Table 4). The chord, from front of carpus to tip of 3rd secondary, varied from 53.0 to 57.5 mm (n = 6). Wing area varied from 136.3 to 157.6 cm²: surprisingly, it was not obviously larger in females, though this might be an artefact of small sample size and the difficulties of making these measurements. For three birds (2 male, 1 female), apparent wing loadings ranged from 0.316 to 0.350 g/cm². Another female was egg-laying when killed and weighed 67.5 g, giving a wing loading of 0.473 g/cm².

For one chick, nearly fledged, chord was 49.5 mm, mass 35 g, and hand length 83 mm; wingspan was 300 mm, and wing area, as measured, was 124.5 cm², suggesting a wing loading of only 0.281 g/cm². Two slightly older, just fledged, young, slightly heavier and with slightly larger wings, had similar wing loadings of 0.310 and 0.285 g/cm² (Table 4). Evidently, the chord attains adult size by fledging. Hand length, and so wingspan, is much lower, but so is mass, resulting in a wing loading that is comparable to (a little below) adult wing loadings. As Fig. 1 shows, wing shape in fledglings is much more rounded, so calculating the areas of the hands as isosceles triangles strongly underestimates their area. The hands of these three were 27.7%, 29.9% and 31.7%, so not only were wingspans lower, but the proportion of wingspan contributed by the hands was also lower.

The change in mass and hand length in all the chicks, and samples of fledglings and adults, is plotted in Fig 2. While hand length increases steadily towards adult sizes as the chicks grow towards fledging over 18–22 days, mass remains at about 40 g. Similarly when mass is plotted against hand length for all age-classes, the otherwise linear relationship flattens at just over 40 g for hand lengths of 100–108 mm, roughly the hand lengths of the oldest chicks and youngest fledglings (Fig. 3).

DISCUSSION

Since the oldest chicks and youngest fledglings have wing areas and loadings that are close to those of adults, their poor flying abilities are not explicable by poor aerodynamic properties. Rather, as Fig. 1 shows, and as the low weights indicate, their bodies are still small; their muscles have probably not fully developed, so they are surely underpowered. Their short, rounded, wings may allow rapid take-off, advantageous for escape from predators, but the short hands imply poor turning ability, and a poor shape for long-distance flight. Therefore as they grow through the fledging period, they make the best of their limited ability to fly by temporarily halting the growth in their mass (Figs 2 and 3). Then,

Table 4. Calculated and measured wing areas for nine individual Common Sandpipers *Actitis hypoleucos* from the Peak District, England.

Age/sex	Mass (g)	Wing area (cm ²)		Calculated/Measured (%)	Wing loading (g/cm ²)
		Calculated	Measured		
Adult male	50.0	128.8	157.6	81.7	0.317
Adult male	48.0	136.3	151.8	89.8	0.316
Adult female	52.0	137.2	148.7	92.3	0.350
Adult unsexed	?	136.9	149.5	91.6	?
Adult unsexed	?	122.1	136.3	89.6	?
Adult female	67.5	128.2	142.7	89.8	0.473
Nearly fledged	35.0	107.4	124.5	86.3	0.281
Fledged	41.0	107.1	132.1	81.1	0.310
Fledged	43.0	124	151.1	82.1	0.285

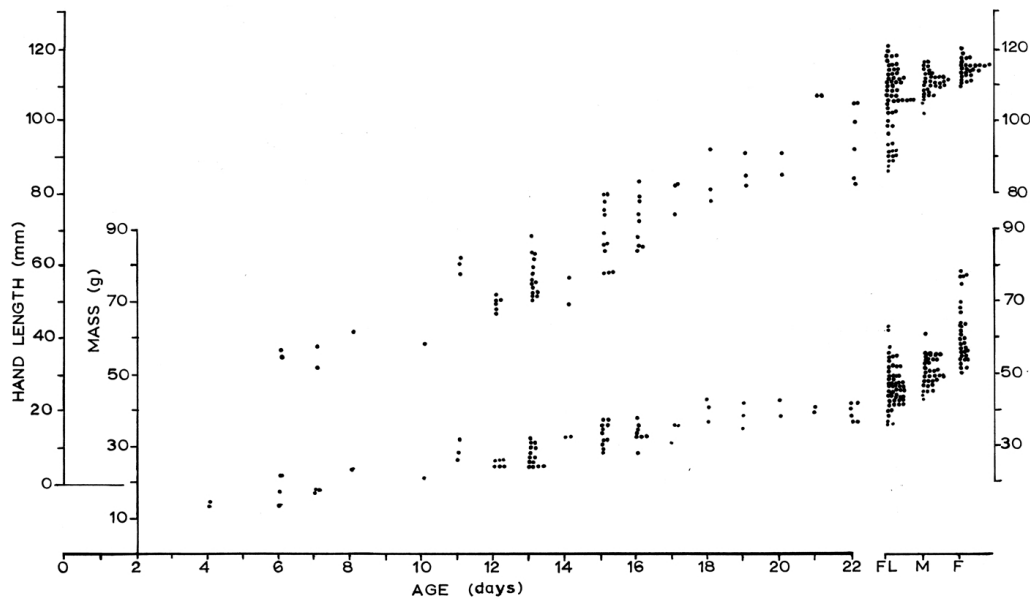


Fig. 2. Plots of hand length and mass against estimated age of Common Sandpiper chicks caught in the Peak District, England, during 1989–2011 compared with samples for fledglings (FL), males (M) and females (F).

as their primary feathers grow during the 2–3 weeks after fledging, they also increase in mass and attain adult proportions before departing their breeding grounds. Presumably their flight muscles also increase substantially as part of this increase in mass.

The adults are also accumulating mass at this time, prior to migration. The females also attain higher than normal mass during egg-laying. Birds trapped on migration at the mouth of the R. Lune averaged 66 g, but the six heaviest were 80–84 g (Dougall *et al.* 2010, Holland 2009), and similar masses were recorded in earlier years at feeding sites near the breeding sites in the Peak District (Holland *et al.* 1982). In this study, the heaviest egg-laying female weighed 91 g on 31 May 2005. Since eggs weigh 12 g, this implies three eggs in the process of maturing. If this heavy adult had a wing area comparable to those measured here, about 150 cm², the wing loading would be as high as 0.607 g/cm², 90% higher than that of adults of more usual weight. This might explain why egg-laying females struggle to fly around mist nets set in their territory with the agility needed to avoid them; it also raises questions about how well-fattened migrants cope.

Carrying unnecessary mass increases wing-loading and energy expenditure; it decreases manoeuvrability and therefore increases the risk of predation. Therefore birds use various strategies for shedding unnecessary mass; for example reducing the size of the reproductive organs at the end of the breeding season. Similarly birds that have already laid down the fat resources they need for migration may reduce the size of their digestive apparatus before departure, building additional flight muscle at the same time (Piersma *et al.* 1999 in relation to Red Knot *Calidris canutus*; Landys-Ciannelli *et al.* 2003 for Bar-tailed Godwit *Limosa lapponica*). In Red Knot, muscle mass has been shown to increase in these circumstances (Dietz *et al.* 2007), but not as much as would be needed to adjust to the increased wing-loading; therefore manoeuvrability was reduced.

Female Common Sandpipers have a slightly but significantly poorer apparent annual survival rate than males (65% v. 76%: Holland & Yalden 1991b), but also slightly poorer site fidelity (79% v. 92%). It has therefore been supposed that the poorer apparent survival rate was caused by a higher rate of emigration, but the higher wing loading of females during

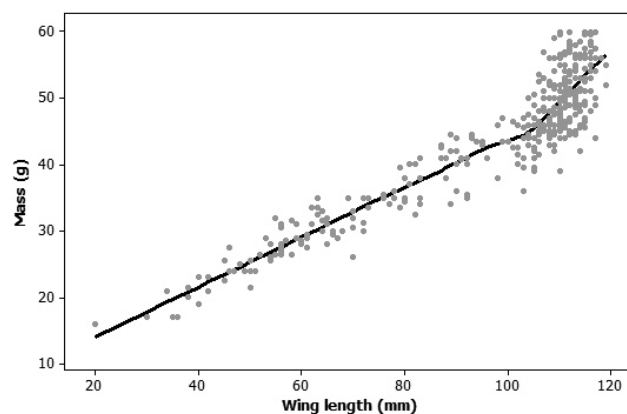


Fig. 3. Plot of mass against wing (or hand length) for all age-classes of Common Sandpipers caught in the Peak District, England, during 1989–2011 (chicks, fledglings and adults), excluding fledglings and adults with a mass of >60 g (i.e. birds laying down resources for southward migration and ovigerous females). The regression line is a Lowess smoother (a locally weighted polynomial regression) that picks up local changes in the relationship between mass and wing length.

egg-laying might make them more susceptible to predation, so increase their mortality rate.

Studies in the English Peak District suggest that adult Common Sandpipers start southward migration from their breeding grounds very soon, apparently within a few days, after completing their breeding cycle (though there are no ringing recoveries in W Africa to confirm this). In comparison young birds seem to depart from Britain more slowly (Holland & Yalden 2002). One explanation for this might be that they require time to develop their wing musculature, though evidently they also use the summer to explore local sites and accumulate fat. Further anatomical studies may be needed before this issue is resolved. Two of the adult casualties studied here had pectoralis major muscle weights (both muscles) of 10 g (20% of its 49 g body mass) and 10.5 g (22% of 48 g). Sacrificing fledglings just to answer this question would not be acceptable, but making use of any accidental casualties from this or other sites might be rewarding.

With a wingspan of about 360 mm, a fat-free mass of 52 g and 30 g of fat, Common Sandpipers should have a still-air flight range of 2,270 km, according to the old program offered by Pennycuick (1989, Program 1). However, that program has been superseded by advances in both physiological and aerodynamic understanding of bird, including wader, migration (Pennycuick 2008). For a start the aerodynamic performance (lift:drag ratio) of waders is better than previously assumed (e.g. Kvist *et al.* 2001), around 11 (rather than 5.5, as calculated by the earlier program). It is also now understood that migrants must burn some protein, as well as fat, and their body mass declines as migration proceeds, changing their aerodynamic performance (Pennycuick & Battley 2003). Pennycuick (2008) shows that the range potential of an impending migrant can be summarised in a single figure, its “energy height”, which is the height in km to which it could climb on the available energy (fat + protein) reserves, and that these are adequately measured as the proportion of the total mass that is fat. One male casualty weighed 0.05 kg, and had a wingspan of 0.36 m with a wing area of 0.0158 m² (the units as needed for *Flight 1.24*). Well-loaded with a nominal 0.03 kg of fat, it would have a fat fraction of 0.03/0.08 = 0.37% fat, and an energy height of 495 km. Its calculated still-air range (at 3,000 m altitude, accepting the other default values) would be 5,893 km, more than enough to take it the 4,000 km to W Africa in one nonstop flight, and allow a good margin for head winds or other mishaps. It would run out of reserves weighing only 39 g. An exhausted Common Sandpiper that was unable to fly and was caught by hand in Ethiopia actually weighed only 30.5 g, though it had recovered somewhat to 43 g after 9 days of feeding (Hillman *et al.* 1986). It was a relatively small bird with a hand length of 110 mm, probably a male; therefore its reserve-free weight would have been less than average.

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