

**AN INVESTIGATION INTO THE RELATIONSHIP OF ABUNDANCE
OF WILLOW WARBLERS *PHYLLOSCOPUS TROCHILUS*
WITH CHANGES IN MEAN WING LENGTHS
OF THEIR POPULATIONS BREEDING IN BRITAIN**

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Abstract

Changes in abundance of species result from changes in stressors acting on their populations. Changes in climate, food availability and predation pressures have been shown to result also in morphological changes in mammals and avian species. Willow Warbler *Phylloscopus trochilus* populations breeding in Britain have declined in abundance since 1985, with their decline more rapid in southern than northern Britain. Using long-term data gathered by ringers, I studied whether Willow Warblers' changes in abundance correlated with morphological changes in their populations. Analysis of changes in mean wing length in the British breeding population as a whole and at five breeding and two migration sites showed that prior to 1985 wing lengths increased as their populations increased in abundance and then after 1985 remained stable or decreased as their abundance declined.

The causes of changes in migratory species are complex. The shifts found in mean wing lengths followed neither Bergmann's nor Allen's rules which would suggest, respectively, a decrease in body size or increase in wing length with the increase in temperature seen this century. Mean male and female wing lengths were highly correlated; this suggests changes in their mean wing lengths are being affected by the same drivers. The trends in mean wing length of Willow Warblers caught in the north and south of Britain after 1985 are similar; this suggests that there is an independent driver(s) causing their different rates of decline in abundance. The presence of a migratory divide within the British population, as in Sweden, might explain differences in changes in abundance between the northern and southern populations, with, potentially, the populations using different over-wintering areas. However, I found no significant differences in wing lengths with increase in latitude so there is no evidence from this study of a similar migratory divide in Willow Warblers breeding in Britain.

Further study of Willow Warbler wing lengths would usefully show whether changes in proportions of males and females present in different populations are driving populations' different rates of abundance. Greater understanding of the location and conditions on their wintering grounds is also needed.

Introduction

This study investigates the hypothesis that decline in abundance of Willow Warblers *Phylloscopus trochilus* breeding in Britain will be reflected in changes in morphology of populations of Willow Warblers, including changes in features that are measured and recorded by ringers. First, information about their life history and changes in abundance of populations is presented as this provides the background to understanding potential causes of changes in abundance or morphology.

Life history

Range and population

Willow Warblers are small insectivorous migrant passerines, weighing approximately 9g (appendix, figure 35). With fossil evidence for presence in the UK from the Pleistocene period (10-120,000 years ago), the species was first named in the UK in 1718 (Bircham 2007). Willow Warblers are amongst the most successful of leaf warblers, with an estimated two million territories in the UK being the most abundant warbler in Britain (www.bto.org.uk 2009) and 31-60 million pairs in Europe, excluding Russia (Burfield & van Bommel 2004). The species has exceptionally large breeding and winter ranges, breeding in Europe and Northwest Asia and wintering in tropical and South Africa (Svensson and Hedenstrom 1999) Two subspecies *P.t. trochilus* and *P.t. acredula* are found in the UK, with the latter passage migrants to Scandinavia and Northern Europe (www.bto.org.uk 2009).

Breeding

Male Willow Warblers return to breeding grounds first, with polygynous males arriving earlier than other male adults who in turn arrive earlier than first year birds (Lawn 1998). Adults show site tenacity, some being caught at the same areas of a trapping site year on year (Pratt & Peach 1991).

More juvenile males return to their natal area than females (Norman 1994). For breeding habitat, Willow Warblers favour scrubby areas, conifers and deciduous woods with open canopy, but with presence of low vegetation, and reedbeds (Lack & Lack 1951; Donald *et al.* 1998) (www.bto.org) and show a preference for Birch *Betula pendula* in woodland. Females usually lay a single clutch of 5-7 eggs, which they incubate for 13-14 days, with chicks taking 13-16 days to fledge (www.bto.org.uk). In June adults and nestlings feed on larvae (Hogstad 1999); females, with their shorter wing lengths are more able to hover than males, capturing prey on the underside of Birch and Willow *Salix sp.* leaves (Nystrom 1991). Birds eat berries in the autumn (www.bto.org). While in active moult after breeding, there is an absence of movement and then juvenile birds begin dispersal in various directions before migration proper (Norman & Norman 1985). Birds which reach adulthood typically live for two years, with adult survival rates calculated at 32% \pm 2% (www.bto.org).

Wintering grounds

Ringling recoveries give little information about Willow Warbler's wintering grounds, with only 14 recoveries south of the Sahara (Salewski *et al.* 2002; Wernham *et al.* 2002). Identification of Willow Warblers' wintering grounds, and study of their winter habitat use is made difficult by their itinerant behaviour. Salewski (2002) describes how Pied Flycatchers *Ficedula hypoleuca* arrive early in the north-east Ivory Coast in September, establish territories and remain in the study area throughout the winter and will return to the same territories the following year. Willow Warblers, in contrast, arrive in November, move through the area in monospecific or mixed-species flocks including resident warblers (Salewski & Jones 2006), are non-territorial, and do not appear to return to a site with ringers registering no re-traps, (although their summer-site fidelity shows they have the ability to return to a site should they wish to) and are absent in January and February, when it is thought they travel further south in search of improved foraging conditions. Salewski *et al.* explain the difference between the two species in terms of their feeding: Pied Flycatchers are more diverse in feeding techniques than Willow Warblers, which are dependent on finding insects on leaves and branches of trees and therefore are forced to be more mobile to find their patchily distributed food.

Migratory staging posts

There is little in the literature about the use of staging posts by Willow Warblers on migration. The comparatively late arrival of Willow Warblers on their wintering grounds in West Africa (Salewski *et al.* 2002) suggests the migratory journey takes a reasonable percentage of a bird's year and so conditions en route will have an important impact on its survival rate. Little is known about the process by which Willow Warblers build up fat stores in preparation for migration from the south of the Sahara in the spring, although it seems to take place in the Sahel area where conditions are least favourable at the end of the dry season (Salewski *et al.* 2002). In some years Willow Warblers arrive in Britain carrying 'pollen horns' after being forced to feed on nectar due to a shortage of insects in North Africa (Steve Stansfield pers.comm.) (figure 1). Results of analysis of samples of pollen have not yet been received, but may assist with identifying passage feeding areas.

Photo: Richard Else



Figure 1. Willow Warbler with pollen horn caught on spring passage on Bardsey Island.

Ringed recoveries suggest that Willow Warblers arrive in Britain in the spring from the south-west, leaving in the autumn from the south-east (Wernham *et al.* 2002). Willow Warblers that arrive on Bardsey Island in the spring, often in large 'falls', spend their time feeding on aphids in the small

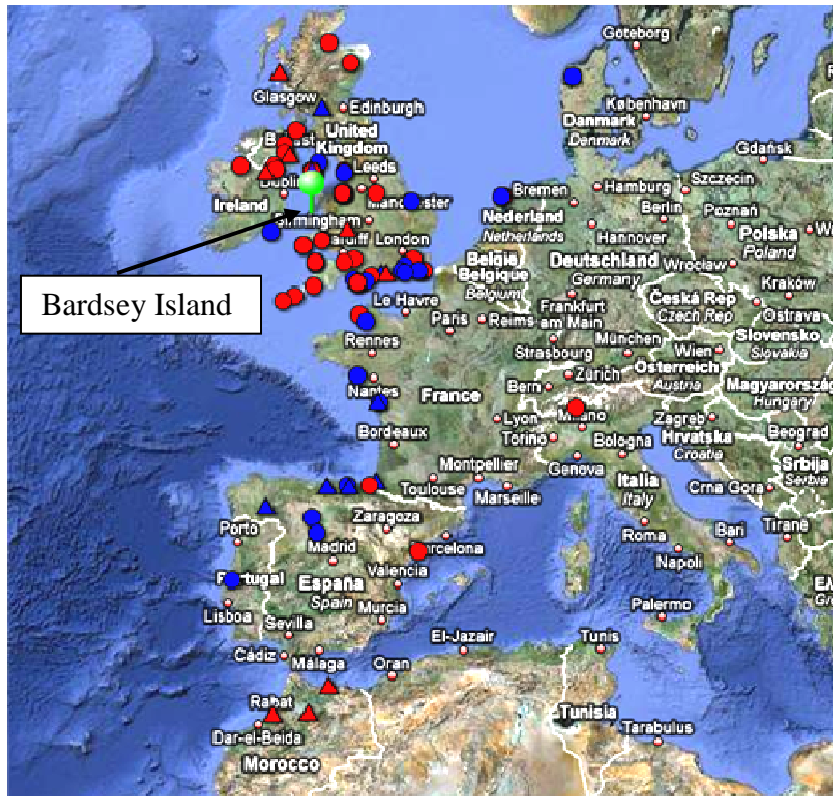
conifer (includes *Picea abies*) plantation and in the Willow beds, before moving on (personal observation). Mapping where birds caught at two of the sites studied for this project, Bardsey Island Bird Observatory and Loch Eye, have been caught elsewhere, and the timing of their catching, illustrates these spring and autumn patterns of movement (figure 2).

Despite migration involving several billion birds of multiple species flying to sub-Saharan Africa (Salewski & Jones 2006), the mechanics of migration are still being discovered. For example, until recently migratory birds were thought to fly non-stop through the Sahara but recent studies by Schmaljohann show that birds rest during the day in the desert and continue migration at night (Schmaljohann *et al.* 2007) and are able to fly at higher temperatures with a lower water rate loss than predicted (Schmaljohann *et al.* 2008). Much is still to be learnt about this aspect of Willow Warblers' life history, which is likely to play a key part in influencing individual's survival rates and hence populations' abundance.

Moult

Willow Warblers are unique amongst Western Palearctic warblers in having a biannual moult, moulting after breeding and on their wintering grounds (Ginn & Melville 1983). The evolution of winter moult may have occurred as birds forage in open sun in Africa and UV light damages their feathers (Svensson & Hedenstrom 1999). The second moult also gives them the advantage of fresh flight feathers for the long journey back to their breeding grounds. However, this does not explain why conspecifics such as Wood Warbler *Phylloscopus sibilatrix* have not made the same adaptation. For this project the presence of this second moult limits the extent to which abrasion confounds analysis of wing length measurements.

(a)



(b)

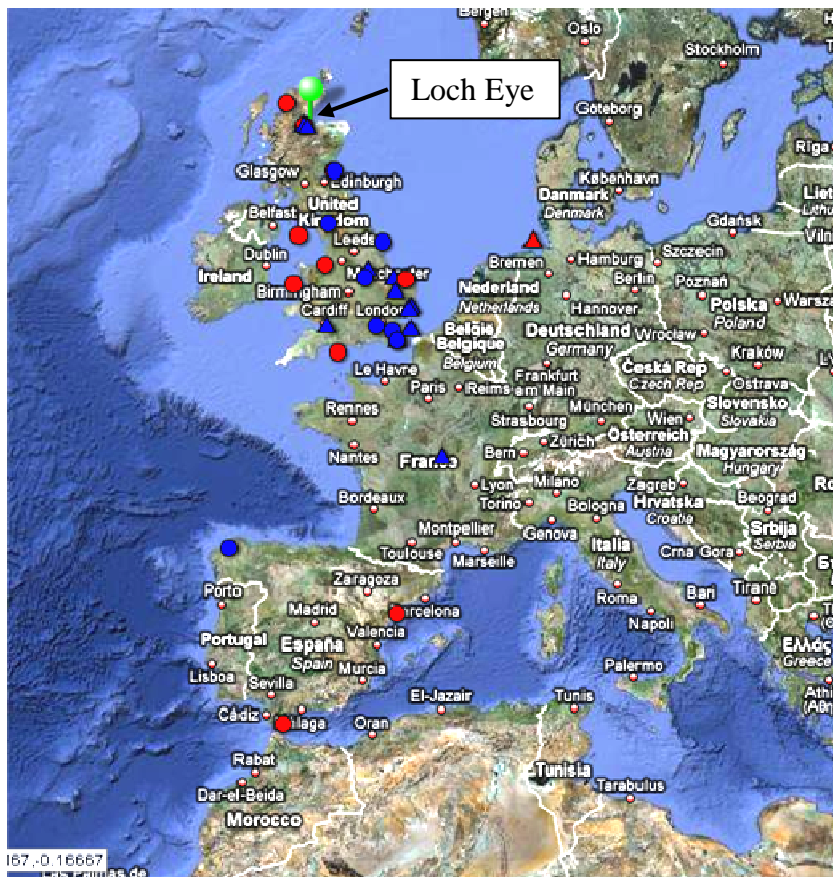


Figure 2. Locations at which Willow Warblers caught (a) on Bardsey Island (b) at Loch Eye have also been caught elsewhere. The shape of the symbols designates the time of year at which birds were caught at the named site: ○ - birds ringed or controlled in March-July; ▲ - birds ringed or controlled in August-October. The colour of the symbols designates the time of year at which birds were found at the location marked by the symbol: red - birds found in March-July; blue - birds found in August – February.

Decline in abundance

Extent of decline

Along with other trans-African migrants (Doswald *et al.* 2009), Willow Warblers' abundance has declined over the last twenty years (www.bto.org.uk 2009) (figure 3).

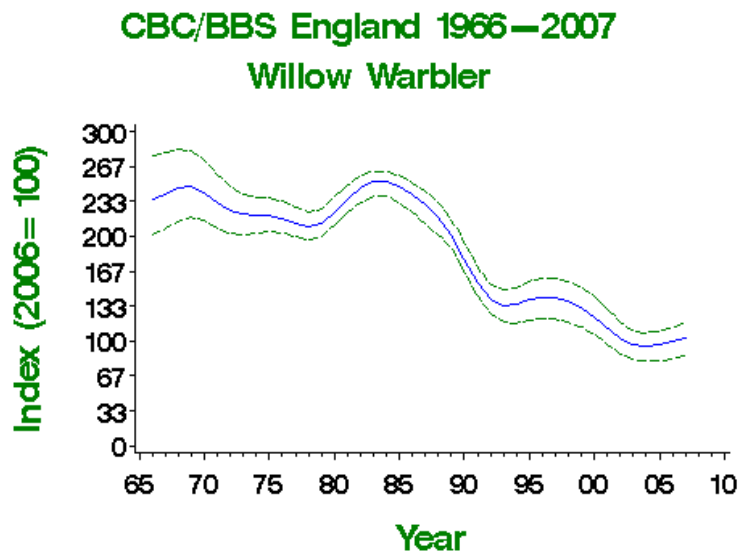


Figure 3. Abundance of Willow Warblers in England since 1965, as measured by the British Trust for Ornithology's Common Birds Census and Breeding Bird Survey, shown with $\pm 95\%$ confidence limits (www.bto.org.uk 2009).

This decline has been more rapid in southern than northern Britain with a decline of 47% between 1986-1993 compared to a decline of 7% in northern Britain in the same period (Peach *et al.* 1995). Results from 1994-2005 from The British Trust for Ornithology's (BTO) Breeding Bird Survey show continued steeper declines in abundance of Willow Warblers in England and Wales than in Scotland and Northern Ireland (www.bto.org.uk 2009) (figure 4). In Europe breeding population numbers have also fallen, on average at a similar rate to that in Scotland (Burfield & van Bommel 2004) (figure 5).

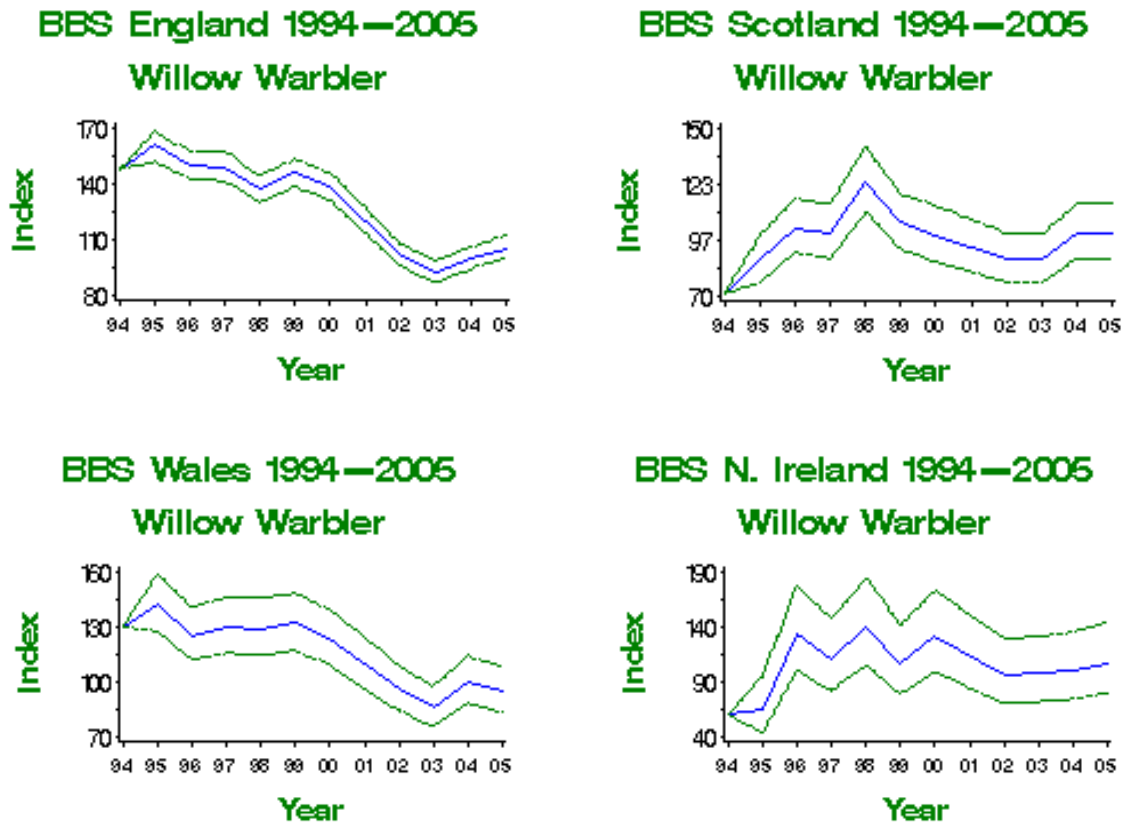


Figure 4. Changes in abundance of Willow Warblers in different parts of the UK, 1994-2005, as measured by the BTO's Breeding Bird Survey, shown with $\pm 95\%$ confidence limits (www.bto.org, 2009).

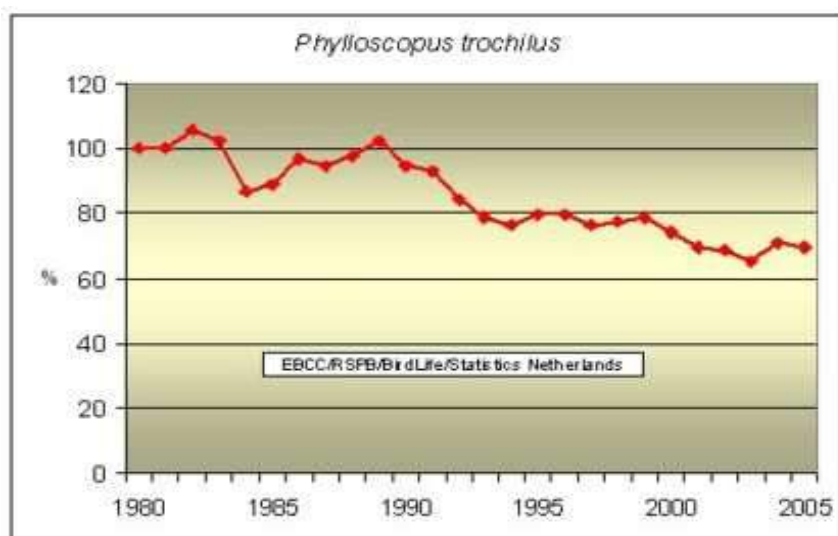


Figure 5. Index of decline in abundance of Willow Warblers in Europe, 1980-2005 (European Bird Census Council 2007).

At Wicken Fen, Cambridgeshire, as an example of changes at site level, decline in abundance of Willow Warblers (with numbers caught calculated as a percentage of total birds caught) reflects national trends in England. However, this result should be treated with some caution as it could be confounded by changes in abundance of other species (figure 6).

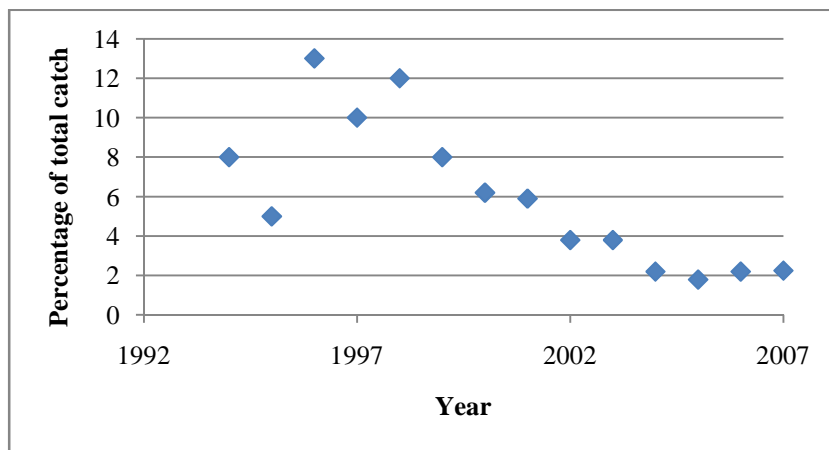


Figure 6. Change in abundance of Willow Warblers at Wicken Fen, Cambridgeshire, 1994-2007.

Abundance of Willow Warblers is calculated as the percentage of Willow Warblers caught of the total catch for the months April – September in each year at Wicken Fen (Wicken Fen Ringing Group data).

Causes of decline

Declines in adult survival rates have probably been a major cause of the overall Willow Warbler population decline for the period 1985-1994, although data from nest record cards suggest an increase in the rate of loss of nests during the nestling stage in 1989-1992 in southern Britain is an additional factor (Peach & Marchant 1995). However, the causes of these declines remain elusive. Since 1998 the BTO's nest record scheme has indicated an increase in Willow Warbler's breeding failure at the egg stage (Leech & Barimore 2008). Between 1939 and 1995 average egg laying dates became a week earlier (Crick & Sparks 1999). This suggests that the species may be responding to changes in temperature but no link between this earlier laying data and increased failure at the egg stage has yet been identified.

The causes of decline in abundance of migratory birds are difficult to identify as they may be a result of changes on breeding grounds, wintering grounds, at migratory staging posts, or of climate change (Newton 2004). Climate, for example, may be changing at a different rate at each of these areas, which may result, for example, in mistiming of birds' arrival for breeding (Both & Visser 2001, Both *et al.* 2006). Over the thirty year period 1970-2000, population decreases have been greater for inter-continental migrant birds than for short-distance migrants or residents and the species with greatest declines are those wintering in dry open habitats in Africa (Sanderson *et al.* 2006). The advantage earlier springs in Britain give short-distance migrants or resident birds, enabling them to establish territories and start breeding earlier, may further disadvantage long-distance migrants (Sanderson *et al.* 2006). Habitat loss may also be a factor in Willow Warblers' population decline. Silver Birch, as a pioneer species, benefited from the destruction caused in woodlands by the 1987 storms and so lack of this habitat is not a reason for Willow Warbler decline (Mason 1997). However, a rise in Roe *Dama dama* and Fallow *Capreolus capreolus* Deer and Muntjac *Muntiacus reevesi* numbers has resulted in a loss of understorey in woodlands, particularly in the south of England where deer numbers are highest, which provides key habitat for Willow Warblers; regional variations in number of deer negatively correlates with regional abundance of Willow Warblers across Britain (Catriona Morrison pers.comm.).

Insufficient is known about the African wintering grounds of Palearctic migrants, to identify the causal contribution of changing conditions on them to population declines of these birds. The Sahel is identified as an important wintering ground and an area where anthropogenic change has resulted in degradation of habitat. But there is no baseline data on habitat use by the different species using this area, so it is difficult to assess the results of habitat changes (Wilson & Cresswell 2006). In the absence of detailed data, surrogates for food availability, such as rainfall (Sanderson *et al.* 2006) and yearly cereal production in Sub-Saharan countries (Eraud *et al.* 2009) have been correlated with annual survival rates on breeding grounds. High survival rates of Turtle Doves *Streptopelia turtur* breeding in western France correlated with years of high cereal production in the Mali-Senegal area (Eraud *et al.* 2009). Years of drought, correlated with low survival rates of Whitethroats *Sylvia*

communis (Winstanley *et al.* 1974). Willow Warblers' itinerant behaviour on their African wintering grounds makes it more difficult to understand effects of changes in climate or habitat in these areas on Willow Warblers' survival rates or subsequent breeding success. In addition, some bird species show differential migration, for example female Chiffchaffs *Phylloscopus collybita* have been found to travel further than males in Europe and North Africa (Catry *et al.* 2005). Should the same differential migration be present in Willow Warblers, the sexes might experience different stresses on migration routes and wintering grounds resulting in different survival rates and potentially in different trends in changes in mean wing lengths as a result of natural selection pressures from changes in climate or food availability.

Impact of changes in climate

Variation in responses with time

There have been major shifts in climate at various times throughout the Earth's history that have led to changes in species ranges or have led to mass extinctions (Sepkoski 1998). Millien *et al.* (2006) summarise the response of organisms to environmental changes resulting from climate changes into three classes: local adaptation and phenological changes; shifts in species' range; local extirpation and extinction (figure 7). Current climate change is considered to be occurring at a greater pace than in previous history with temperature increases of c.0.6°C during the 20th century (Houghton *et al.* 2001). Over the last 20-30 years an increase in temperature has led to advancement of phenology of plants and invertebrates (Jonzen *et al.* 2006), with, for example earlier breeding dates for a number of species of birds (Crick & Sparks 1999), and this rate of change may be faster than organisms can adapt to (Barnosky *et al.* 2003, Davis *et al.* 2005) leading, for example to mismatching of timings of breeding and food availability. Pied Flycatchers, which are long distance migrants, have not changed their arrival date in breeding grounds but have advanced their laying date, but not sufficiently to match the change in phenology on the breeding grounds induced by climate change (Both & Visser

2001). In addition species have shown range shifts, changes in body size and changes in the strength of competition between species (Visser 2008). Much work is still to be done to discern how far these changes are plastic responses or are evidence of microevolutionary responses to climate change (Gienapp *et al.* 2008), and Gienapp warns of the danger of ‘the fallacy of adaptive story-telling’.

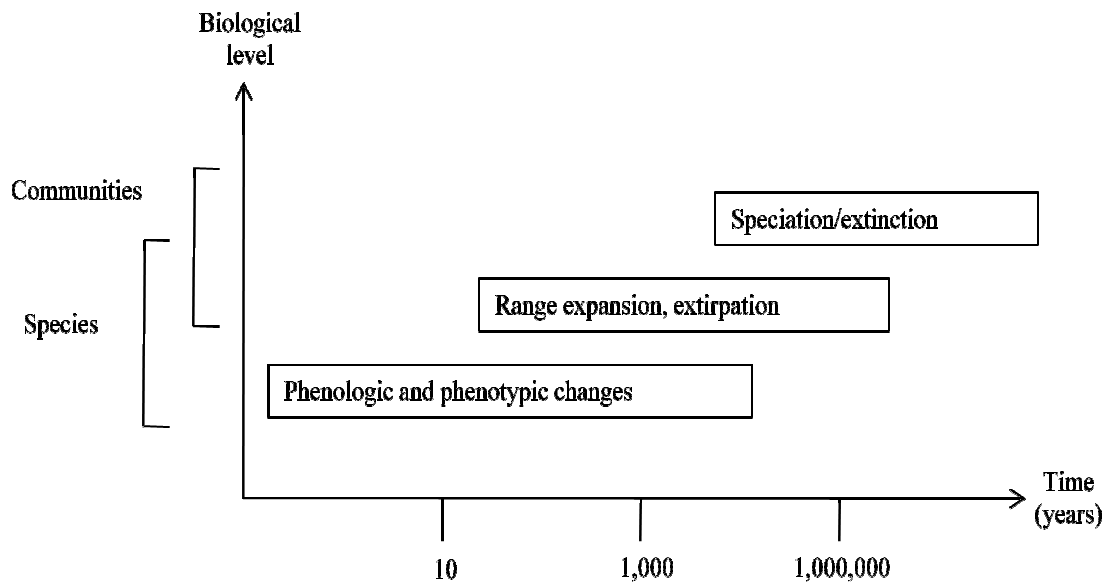


Figure 7. Temporal scales of biological responses to climate change. From Millien *et al.* (2006).

Changing patterns of migration

Migration is widespread across the animal kingdom as a means of exploiting resources and avoiding deterioration of resources (Zink 2002). Willow Warblers are amongst the billions of birds that migrate between their breeding grounds in the Western Palearctic and their wintering grounds in Africa (Newton 2004). Understanding the origin of migration and its mechanisms will assist in understanding possible influences and responses to these influences in bird populations today.

For Palearctic bird species, it is debated whether migration evolved in tropical sedentary birds, with population pressure forcing polewards shifts of breeding ranges, with birds returning to their place of origin as resources declined (the southern home theory) (Rappole *et al.* 2003, Zink 2002), or whether migration originated with birds breeding in the north forced south with decline of resources in the

winter (Gauthreaux 1982, Bell 2000). Bruderer and Salewski (2008) argue that both explanations fail to consider the effect of numerous climactic changes in the glacial periods and that the evolution of migration is related to climate changes on breeding grounds, with range expansion and shifts induced by climate variation. Louchart (2008) supports this approach arguing for neither a northern or southern home origin of migration but instead for an understanding of migration in the shifting climatic context in which it developed, with ancestral breeding homes 'shifting' across high and middle latitudes with changes in climate. Louchart (2008) argues that current shifts of birds' winter ranges, coinciding with climate change, with the majority resulting in a decrease in average migration distance, support this 'shifting home' theory (Rappole *et al.* 2003).

Current shifts in migration patterns, whether of distance, direction or timing, also show that migratory changes can be rapid through microevolutionary processes (Salewski & Bruderer 2007). Experiments with breeding captive Blackcaps *Sylvia atricapilla*, for example, have shown that in a few generations the direction of migratory restlessness is changed (Berthold *et al.* 1992) and migratory divides have evolved (Bearhop *et al.* 2005). Poleward shifts have been found in the winter ranges of North American birds (Bearhop *et al.* 2005, Barbet-Massin *et al.* 2009). Some short distance migrants to Britain have decreased their migration distance (Visser *et al.* 2009) and some long distance migrants are arriving earlier on breeding grounds (Jonzen *et al.* 2006).

For Willow Warblers, along with other long distance migrants, the Sahara is a barrier to flexibility both in winter migration ranges and timing of return in the spring. This barrier may prevent them making the adjustments to their wintering range that with warmer temperatures, would enable them to have the advantages of travelling less far, to arrive back early in spring and be better able to estimate the advancement of spring at higher latitudes, and so remain competitive with residents and short distance migrants which have these advantages (Louchart 2008).

For other migrants, either their migratory strategy has not changed, depending on endogenous rhythms that are not affected by climate change (although the shift in Blackcaps migratory range

suggests otherwise) or climate change in wintering grounds does not match that in the breeding grounds, preventing species making adequate adaptations (Both & Visser 2001). However, it is possible that birds delay spring migration when wintering conditions in Africa are good, and then speed up migration through Europe, so there is some scope for flexibility in the migration process (Tøttrup & Thorup 2008, Tøttrup *et al.* 2008). If Willow Warblers in different parts of the UK follow different migratory routes or have different wintering grounds, climate change may operate differently along the routes or at the wintering grounds and so affect the populations differently.

Changes in morphology following Bergmann's and Allen's rules

Bergmann's rule, first described in 1847, identifies the tendency of endothermic animal species within a genus to be larger in body size as temperatures decrease, the difference is driven by the reduction in heat loss being proportional to surface to volume ratio of an organism (Millien *et al.* 2006). Therefore, with a warming climate the expectation is that the body size of organisms will decrease. Allen's rule describes the tendency of species to have reductions in size of appendages, such as ears or limbs, with decrease in temperature, to reduce heat loss in cold temperatures and longer appendages in warmer climates to increase heat dissipation (Moreno-Rueda & Rivas 2007). In examining these rules, latitude is frequently used as a surrogate for environmental temperature, with which it is closely correlated (Olson *et al.* 2009).

There has been much debate over the extent to which Bergmann's and Allen's rule can be applied. Meiri & Dayan (2003) argue that sedentary rather than migratory species are more likely to conform to Bergmann's rule as migratory birds avoid the more extreme temperatures that drive conformity. Olson *et al.* (2009) argue that latitudinal trends in body size are stronger when based on wintering rather than on breeding ranges of species if the body size is small as that is where species are encountering more extreme climatic conditions. Drivers to conformity to Bergmann's rule other than heat conservation have been suggested, for example fasting endurance in cold climates with limited food availability (Ashton 2002). Baker (1980) found a latitudinal trend in size in House Sparrows

Passer domesticus in the hundred years since they were introduced in New Zealand, with more recently Monahan (2008) identifying a trend of decreasing wing length with increasing winter temperature; Yom-Tov *et al.* (2006a) found body size of Otters *Lutra lutra* in Norway is positively correlated with latitude and found increases in wing length in 6 out of 7 bird species at Wicken Fen as would be expected by Allen's rule (Yom-Tov *et al.* 2006b). However, while finding no change in residual body weight of Willow Warblers, Yom-Tov found what he describes as an unexpected decrease in their residual wing lengths.

When considering effects of climate change on wing lengths of birds, Bergmann's and Allen's rule are counterintuitive: a colder climate requires a larger body, which would require longer wings for flight aerodynamics and additional heat insulation, while according to Allen's rule a colder climate requires shorter appendages for heat insulation. If wing lengths of species are a function of body size (Monahan 2008), following Bergmann's rule they would be expected to decrease in a warming climate. However, following Allen's rule, they would be expected to increase in a warming climate. Great Tits *Parus major* and Blue Tits *Parus caeruleus*, two of the three species, Yom-Tov reports as decreasing in residual body weight at Treswell Wood, the other site included in his study (Yom-Tov *et al.* 2006b), also show linear decreases in residual wing lengths. This may suggest that Bergmann's rule sometimes has priority. In Yom-Tov's study six of the total fourteen species showed decreases in body weight, as would be expected by Bergmann's rule. Increases in wing length were shown in nine of the fourteen species, as would be expected in Allen's rule. These rules therefore are not necessarily good predictors of changes in individual species.

Changes in morphology with food availability and predation pressures

Olson *et al.* (2009), in their global scale analysis of avian conformity to Bergmann's rule, found that while temperature is the single strongest environmental correlate of body size, there are strong secondary correlations such as resource availability and species richness. These could in themselves be indirect effects of changes in climate as shifts in temperature and/or precipitation have indirect

effects on habitat and food supply (McCarty 2001). Stenseth (2002) argues that effects of climate change on organisms are complex and operate both directly on species' physiology; and indirectly through changes in the ecosystem inhabited by the species, the latter through changes in prevalence of prey, predators and competitors. In turn, the extent of influence of these changes depends on the size of individuals, their sex and age; the frequency of extreme climactic events, rather than necessarily fluctuations in the mean climate; and interactions with other factors, for example density dependence. Habitat fragmentation adds a further stressor: with the huge increase in the human population, of 1.6 billion to over 6 billion in the 20th century, having an effect on the environment at a rate at least as fast as the population increase (McCarty 2001). Research focussed on individual species has shown that body size of Finnish male and female Goshawks *Accipiter gentilis* have decreased and increased respectively in relation to size of prey available ((Tornberg *et al.* 1999, Yom-Tov & Yom-Tov 2006c); Dippers *Cinclus cinclus* size has changed in relation to water levels (Moreno-Rueda & Rivas 2007); Great Tit body weight and wing lengths correlated with predation pressure from Sparrowhawks *Accipiter nisus* (Gosler *et al.* 1995) and early nutritional provision of Song Sparrows *Melospiza melodia* reduced their adult skeletal size (Searcy *et al.* 2004).

Possible presence of migratory divide within the Willow Warbler population in Britain

Willow Warblers breeding in Sweden have been found to represent two sub-species *P.t. trochilus* and *P.t. acredula* with size and coloration differences. The presence of a migratory divide in central Scandinavia (62° and 63° N latitude) is not associated with habitat differences (Bensch *et al.* 1999, Bensch *et al.* 2009). Although precise wintering grounds cannot yet be identified, stable isotope analyses of feathers have confirmed that southern birds migrate to West Africa while northern birds migrate to East and South Africa (Chamberlain *et al.* 2000, Bensch *et al.* 2006). There is some evidence that, amongst different populations, those with longer wings migrate further (Fiedler 2005). If Willow Warblers in the north and south of Britain are found to have different mean wing lengths this would be an indication that there might be a migratory divide in the population and that, like the Swedish populations, they may have different wintering areas, with potentially the longer winged

birds travelling furthest, and differences in wintering areas and migration routes might contribute to the difference in the rate of decline in abundance of Willow Warblers in the north and south of Britain.

Relationship of wing lengths of Willow Warblers and their decline in abundance

I investigated whether there are differences in, or have been changes to, mean wing lengths of populations of Willow Warblers breeding in different parts of Britain and, if such differences or changes are present, whether they can contribute to understanding Willow Warbler populations decline, and/or the regional variation in their decline, in Britain since 1984. I analysed wing length data collected by ringers across Britain over a period of more than forty years and predicted that there would be differences in mean wing lengths of populations of Willow Warblers with latitude; that stresses on populations, directly or indirectly as a result of climate change or habitat fragmentation, shown in decreases in abundance, would be reflected in changes in mean wing length; and that the direction and size of any changes in wing lengths would be similar in male and female birds from the same populations.

Methods

Locations from which data has been analysed

For this study wing length information from adult Willow Warbler ringing data held by the British Trust for Ornithology from across Britain from the period 1967-2008 is analysed (appendix, table 3).

To investigate possible differences at local level, data is also analysed from five breeding sites (appendix, table 4) and two sites where birds are caught on migration (appendix, tables 5 & 6).

The breeding sites are at: Loch Eye, Highland; Kippo Wood, East Fife; Wicken Fen, Cambridgeshire;

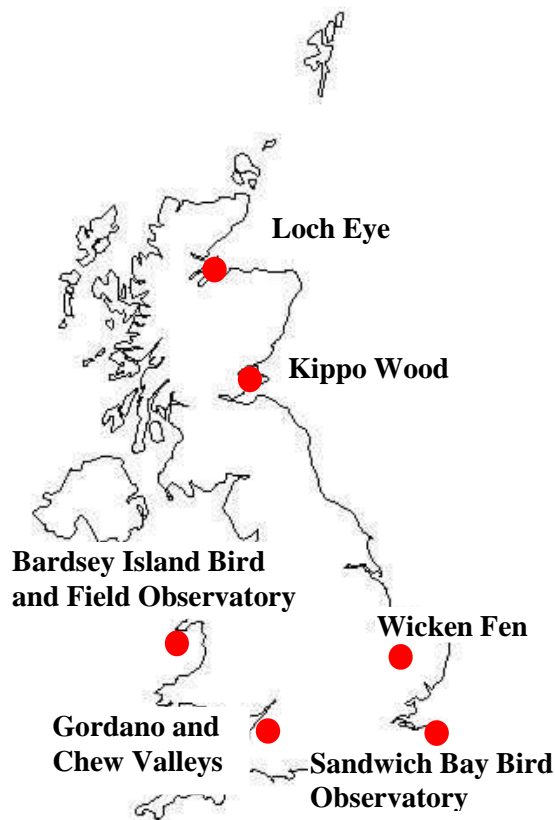


Figure 8. Location of individual sites from which data has been analysed.

and two sites from North Somerset: Chew Valley and Gordano Valley, whose results are combined; the two sites where birds are caught on migration are operated by Bird Observatories: Bardsey Island, off the Llyn Peninsula and Sandwich Bay, Kent (figure 8).

Breeding sites were selected that each had over 1,000 computerised records of adult Willow Warblers caught during a period of 10 years or more and that represented different geographical locations around Britain. Results from Chew Valley and Gordano Valley sites, situated 12 miles apart, were combined to have sufficient records for analysis by Bhattacharya's method as implemented in FISAT software (see below). Migration sites were chosen for their location to the west and to the

south-east of Britain and because, as a result of commitment to regular ringing operations, they have large long-term datasets. If Willow Warblers breeding in Britain use different migration routes, the

geographical location of the migration sites to the west and south-east of Britain optimises the chances of their inclusion in the data analysed. Recovery data show birds caught at these sites breed at all latitudes in Britain to their north, therefore results of analyses of data from birds caught at these migration sites should reflect any differences or changes in wing length found in populations at breeding sites (figure 2a and 9).

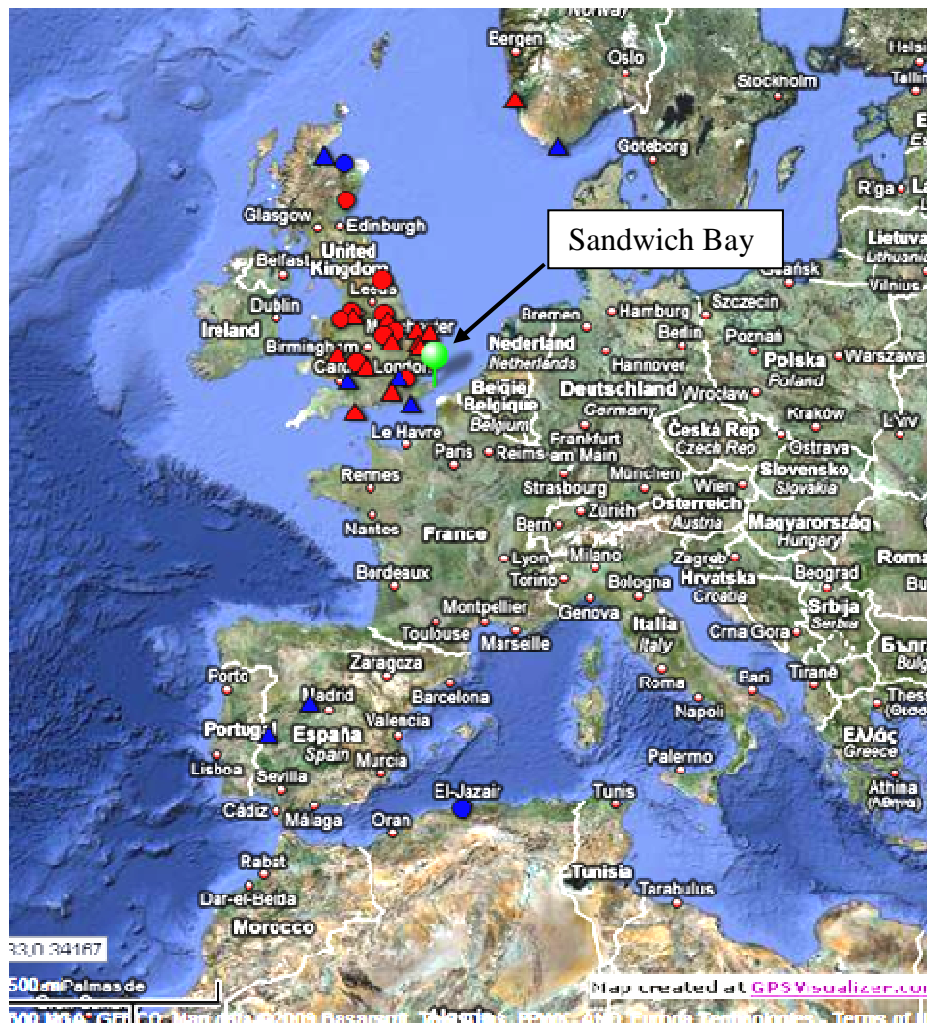


Figure 9. Locations at which Willow Warblers caught at Sandwich Bay have also been caught elsewhere. The shape of the symbols designates the time of year at which birds were caught at Sandwich Bay: O - birds ringed or controlled in March-July; ▲ - birds ringed or controlled in August-October. The colour of the symbols designates the time of year at which birds were found at the location marked by the symbol: red - birds found in March-July; blue - birds found in August – February.

Habitat varies at each of the ringing sites although at all Willow *Salix sp.* scrub is present. Loch Eye's site has a small area of deciduous wood with much willow scrub and ground vegetation edging the Loch (Bob Swann, pers. comm.); Kippo Wood has been largely clear felled and planted with Larch *Larix deciduas* and Sitka *Picea sitchensis* but has large areas of unplanted Willow and Birch scrub (James Cobb, pers.comm.); Wicken Fen is remnant fen and includes Reed *Phragmites australis* and Sedge *Carex sp.* beds and willow scrub; the Chew Valley site is on the naturalised margins of a reservoir with reed-bed merging into sedges and Willow carr (Mike Bailey, pers.comm.); the ringing site within the Gordano Valley is lowland wet scrub with Reed, Rush *Juncus sp.* and Sedge (Lyndon Roberts, pers.comm.). Sandwich Bay Bird Observatory operates on a coastal site, which, in the past had little vegetation. Trees have now been planted to provide cover and most of the Willow Warblers have been caught in very small areas of deciduous trees, within 150m of the shore (Keith Ellis pers.comm.). On Bardsey Island, Willow Warblers are largely caught in small areas of Willow scrub and in a small coniferous plantation; (personal observation).

Accessibility of data from sites

There has been a huge increase in the number of records held on computer by the BTO since the mid-1990s, with only 4% of computerised records from the period before 1986 (figure 10). For this study I needed data from before 1985, when the recent decline in Willow Warblers' abundance began and therefore this project was made possible by the recent computerisation of all paper records of birds caught at Bardsey Island and Sandwich Bay Bird Observatories. To extend data accessible for analysis from Wicken Fen I computerised over 1700 records of Willow Warblers for the period 1968-1990. These last 3 datasets are not yet included in the data held by the BTO (2008).

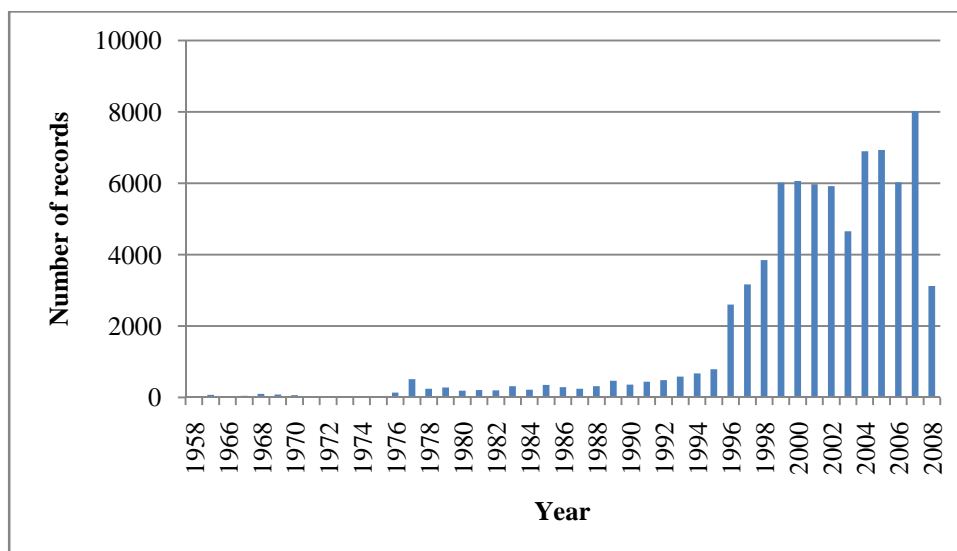


Figure 10. Number of computerised records of adult Willow Warblers caught in Britain with wing length data held by the BTO, 1958-2008.

Wing length chosen as morphological feature for analysis

Wing length (mm) is the measurement most frequently recorded by ringers in the time period for which data is required for this study and is usually recorded to the nearest 1mm and taken using the maximum chord method (Redfern & Clark 2001).

Avoiding confounding of data

Wing length measurements give problems with repeatability. This is to some extent met in this project by using, where possible, the mode of any wing lengths of birds for which there are multiple captures in a period (week, month, year) (for example, if on first capture of a bird a wing length has been measured as 65mm and on subsequent recaptures as 67mm and 67mm, the mode of 67mm has been used.) Where only two captures have been made, or a mode is not possible, the average of the wing length has been calculated, rounded to the length of the earliest capture. Results are rounded to the nearest integer as Battacharya's method, used to calculate male and female mean wing lengths,

requires even distribution of wing lengths and sufficient counts in each to separate the two populations. This method also prevents data from multiple retraps of an individual bird skewing results.

Only wing length data for adults, or first year birds after they have completed their full winter moult, have been included as juveniles have a shorter wing length than adults (adult mean 66.3 ± 4.4 (mm), juvenile 64.8 ± 2.8 (mm) (www.BTO.org.uk) (figure 11). Nest records for Willow Warblers show an average of 12th May for completion of clutches, with the earliest recorded clutch completed on the 2nd May. Allowing for the shortest incubation and fledging periods of 13 days each (Joys and Crick 2004), a young bird of that year is very unlikely to be caught before 1 June, and, if it is, will be identifiable as a juvenile. Therefore to include as many records as possible, birds aged as 2 (of unknown age) before 1st June have been included as almost certainly a second year bird or adult.

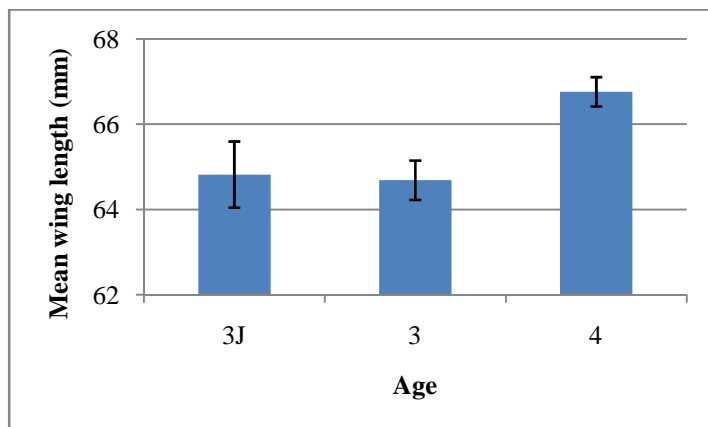


Figure 11. A comparison of mean wing lengths of juvenile and adult Willow Warblers ringed at Wicken Fen, 2000-2008, (n=477) using ringers' ageing scheme (age 3J is a bird still partly or completely in juvenile plumage, age 3 is a bird hatched in the calendar year in which it is caught, age 4 is a bird hatched before the current calendar year (Redfern & Clark 2001).

Some Willow Warblers commence moult in early June (Ginn and Melville 1983). Data from all birds with a moult primary score over 20 have been excluded to ensure there is no possibility that the second primary (which gives the wing length) is in moult and therefore 'falsely' short.

Svensson (2005) gives an adult wing range of 60-70 mm for Willow Warblers, however, 3.6% of wing lengths recorded in ringing data held by the BTO are outside this range. Willow Warblers are occasionally mistaken for Chiffchaffs. The majority of Chiffchaffs are smaller and have darker coloration than Willow Warblers, but some birds are similar in size and colour to Willow Warblers (figure12). Ringers differentiate Willow Warblers from Chiffchaffs in the hand by the absence of emargination on the 6th primary and differences in the primary feather that forms the wing point (Svensson 2005), however errors are occasionally made. In addition, ringers occasionally make mistakes in measuring, reading or recording a wing length (Chris Thorne pers.comm.).



Figure12. Willow Warbler (left) and Chiffchaff (right) caught on spring migration on Bardsey Island.

While needing to avoid such errors from confounding results, in order to identify possible changes in mean wing lengths within the species it is necessary to include data that fall outside expected ranges. Wing lengths have therefore been included which have a count $> 0.05\%$ (so within 95% confidence limit) of the total records selected for analysis ($n=76,886$), which is all wing lengths $>55\text{mm}$ and $<75\text{mm}$.

Willow Warblers are unique for passerines breeding in the UK as they moult twice a year, once in their winter quarters and again after breeding (Ginn and Melville 1983). This reduces the effect of abrasion on the length of their primary feathers through the year. However, from arrival in Britain in April to commencing moult in July, mean wing lengths of males and females decrease by approximately 0.5mm (table 1). To reduce the effect of abrasion on analyses of mean wing lengths, for breeding sites only data from birds caught between April to June inclusive have been included.

Table 1. Mean wing lengths (mm) of male and female adult Willow Warblers by month calculated from BTO data, 2004-2008.

Month	Male				Female			
	Mean wing length (mm)	Standard error	Difference in wing length to previous month	Count	Mean wing length (mm)	Standard error	Difference in wing length to previous month	Count
April	68.99	0.02		4414	63.77	0.03		2905
May	68.77	0.04	-0.22	1633	63.76	0.03	-0.01	2349
June	68.59	0.04	-0.18	1170	63.57	0.06	-0.19	752
July	68.45	0.07	-0.14	394	63.31	0.07	-0.26	740
August	68.43	0.07	-0.02	599	63.56	0.08	0.25	638
September	68.43	0.30	0.00	47	64.00	0.19	0.44	99

Limiting data included to that from April-June also optimises the possibility that any bird caught is a breeding bird rather than a passage migrant (Newton 2008) and reduces the possibility that a juvenile is mistakenly included as an adult.

Data from birds on spring migration only are included

Willow Warblers caught at migration sites in the spring and autumn could represent different populations, or different members of the same populations either taking different migration routes to and from the UK and Ireland or requiring use of different staging posts and therefore data from spring and autumn birds needs to be analysed separately. At both sites there is insufficient data from birds on autumn migration and therefore data from birds on spring migration only are analysed.

Mean wing lengths for male and female Willow Warblers are calculated separately

Potential confounding of results if proportions of each sex included in data changes

A histogram of count of Willow Warblers' wing lengths shows their bimodal distribution, with males and females having different but overlapping wing length ranges (figure 13).

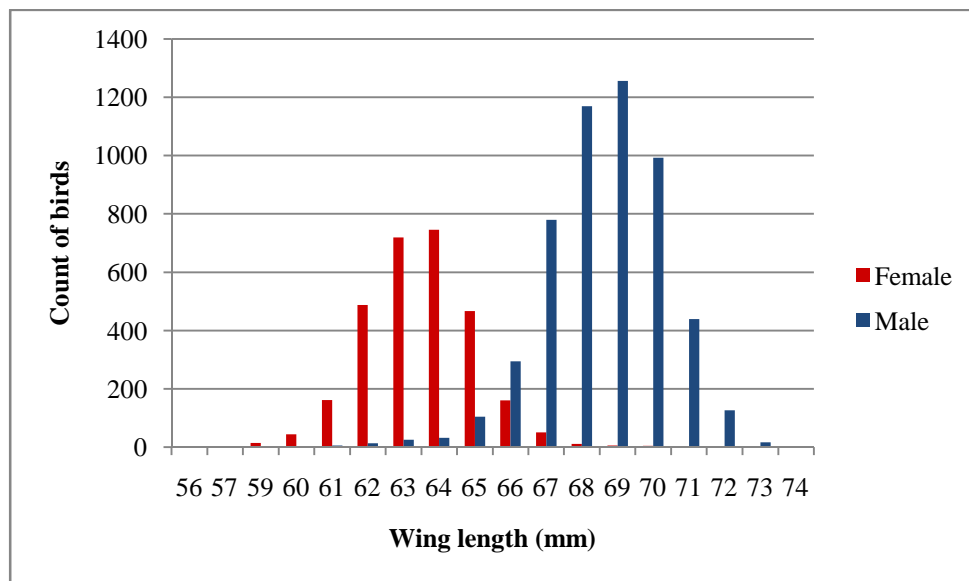


Figure 13. Wing lengths of male and female Willow Warblers, sexed by brood patch or cloacal protuberance, from all BTO data, 1973-2008.

Therefore, analyses of mean wing lengths of Willow Warblers for a particular site or period are skewed if different proportions of male and female Willow Warblers are caught at different times.

The count of wing lengths of birds caught changes as the proportion of each sex caught changes during the breeding season (figure 14). In April predominantly males are present; in May females are present but the proportion of females caught is probably less than males as the females are incubating clutches; in June, males and females are both caught probably as they hunt for food to feed their chicks; in July, males and females start to moult, this probably results in less activity and fewer of both sexes being caught.

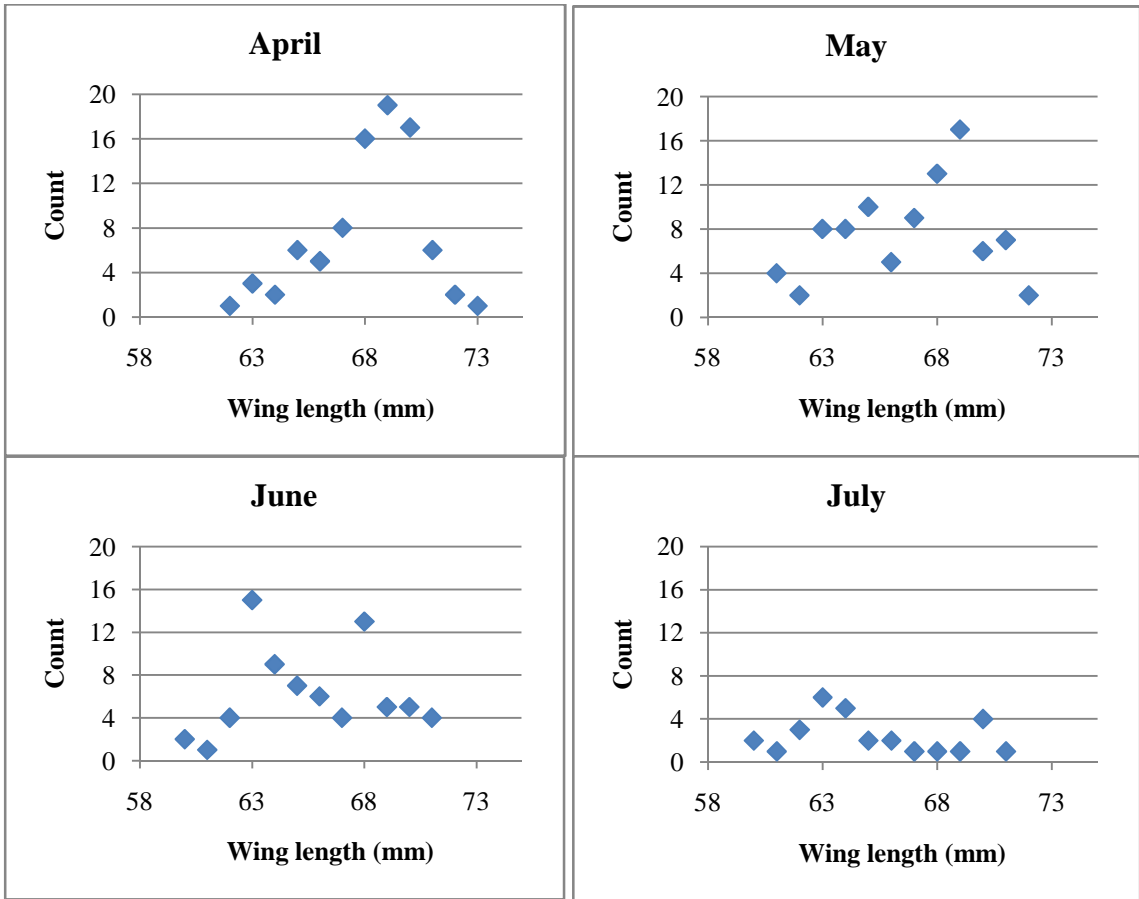


Figure 14. Count by month of wing lengths (mm) of adult Willow Warblers caught at Wicken Fen, 2000-2008.

At migration sites there are also changes in proportions of males and females caught as spring or autumn passage progresses. Wing lengths of Willow Warblers caught at Bardsey Island in spring show male Willow Warblers arrive first, with females following (figure 15). The change by week in the proportion of male and female Willow Warblers caught on spring migration at Bardsey results in a decrease in mean wing length of up to 2.3 mm a week and over a 5 week period of 4.8 mm (figure 16). Differences in timing, or success, of ringing effort at migration sites would therefore confound any analysis of Willow Warblers mean wing lengths unless separate means for male and female wing lengths are calculated.

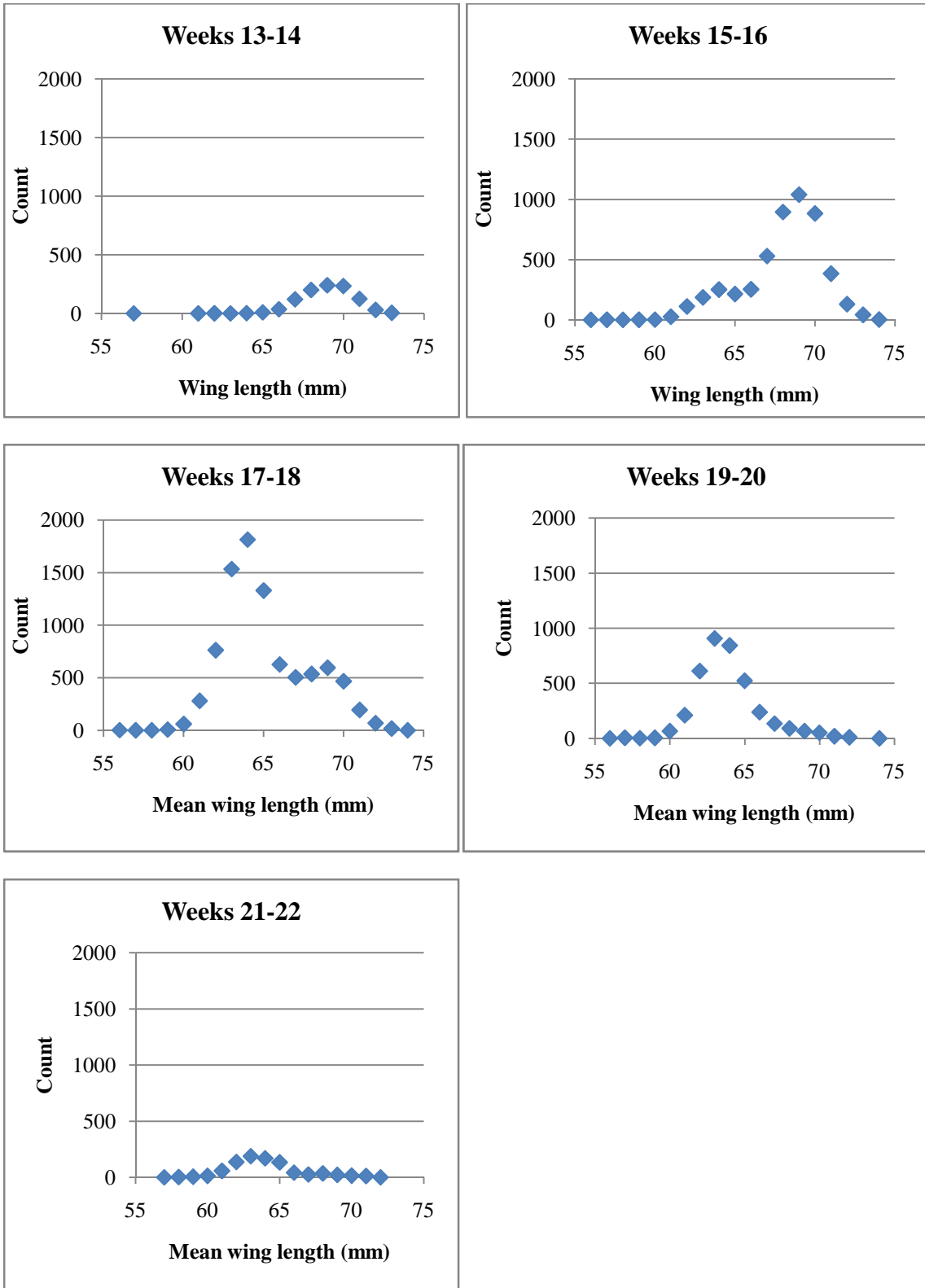


Figure 15. Changes in fortnightly count of wing lengths of adult Willow Warblers caught on spring passage at Bardsey Island, 1956-2008 (week 1 = 1st week of January).

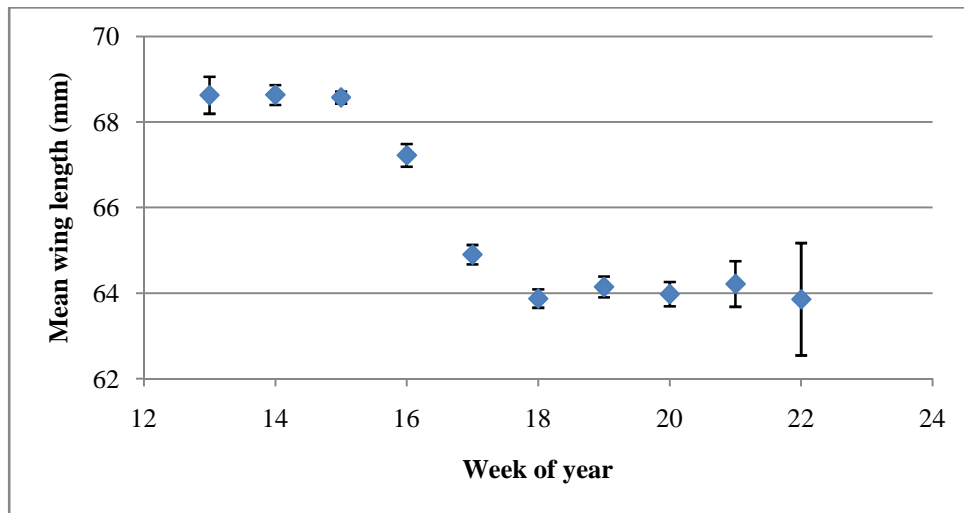


Figure 16. Changes in mean wing length (mm) by week of year of adult Willow Warblers caught at Bardsey Island, 1998-2007 (shown with $\pm 95\%$ confidence intervals, week 1 = 1st week of January, n=2676).

Method for calculating male and female mean wing lengths

Male and female birds are identical in appearance. Their wing length ranges overlap therefore the only reliable method for separating Willow Warblers in the hand is during the breeding period by presence of a cloacal protuberance, for a male, or a brood patch, for a female (Svensson 2005). Analysis of wing lengths of birds sexed by sexual characteristics suggests (without making assumptions about error by ringers in correct identification of sexual characteristics) that only birds with short ≥ 62 (mm) or long ≤ 69 (mm) wing lengths can be sexed by wing length (figure 13). Of the 76,890 ringing records of adult Willow Warblers held at the BTO, just over 60% are assigned a sex, but for these birds approximately half have no method recorded for how they were assigned a sex and nearly a fifth have been assigned a sex on the basis of size alone. Under a third of birds caught in the breeding season have been assigned a sex by presence of sexual characteristics.

Results after bootstrapping (100 times) different sample sizes (10-90) of wing lengths of (i) male (n=213) (ii) female (n=308) adult Willow Warblers, caught at Wicken Fen, that had been sexed by presence of sexual characteristics, and calculating mean wing lengths for each sample showed that

sample sizes of at least 40 females and 40 males are required to achieve 95% confidence in identifying changes in mean wing length of 0.5mm ($0.25 \times 1.96 = 0.49\text{mm}$) (figure 17).

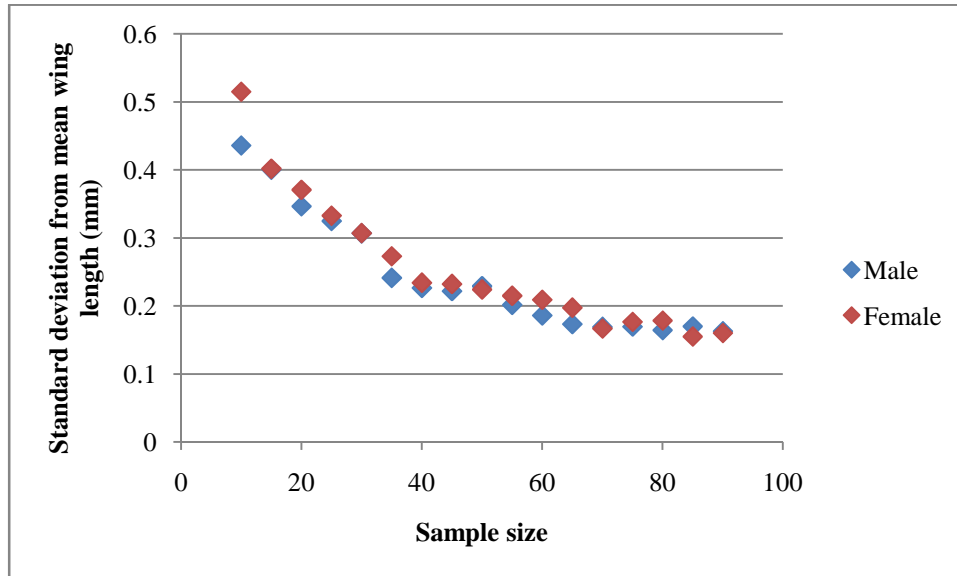


Figure 17. Standard deviations of mean wing lengths (mm) of adult male and female Willow Warblers caught at Wicken Fen from calculated from analyses of different sized samples (each bootstrapped 100 times).

Even for sites where ringers have identified the sex of individual Willow Warblers using the presence of sexual characteristics, the number available for analysis is therefore too small to identify changes in mean lengths by year with confidence. Therefore Battacharya’s method, as implemented in the software programme, FISAT_II designed for the analysis of length-frequency data of fish stocks, has been used to calculate separate male and female mean wing lengths and counts of males and females from samples of Willow Warblers. First Bhattacharya’s method is used to separate samples into normal distributions of male and female and then NORMSEP is used to refine the calculated mean wing lengths and sample sizes for each distribution (www.fao.org/fi/statist/fisoft/fisat/index.htm) (appendix, figure 36).

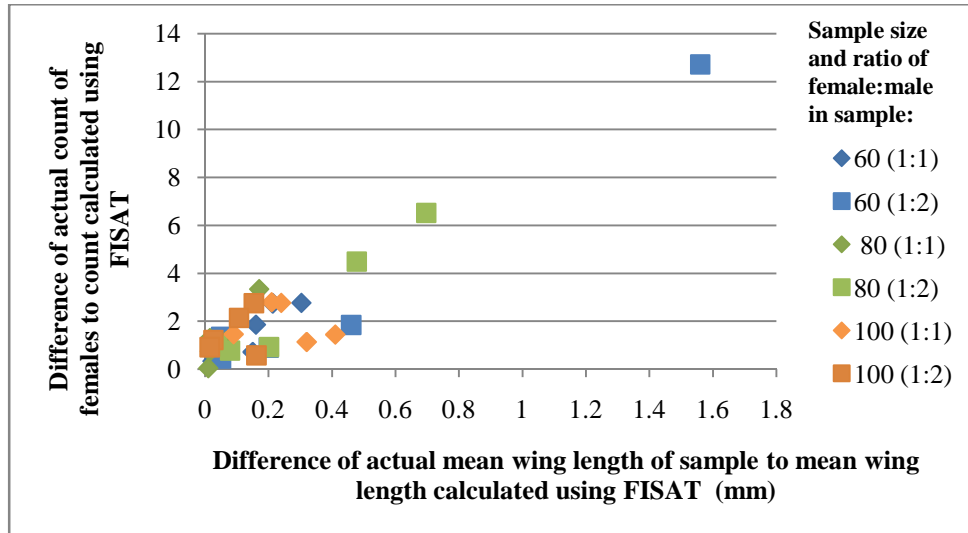
To ascertain the sample size required to calculate mean wing lengths to the optimum level of confidence using FISAT (i.e. identifying when increasing sample sizes are not matched by an

increasing level of confidence in results), samples of wing lengths of 60, 80 and 100 Willow Warblers, sexed by sexual characteristics, caught at Wicken were bootstrapped (10 times). (It was assumed that the sample size would need to be larger than the sample size of 40 birds required for calculating, to the confidence level required, the mean wing length of samples of known male or known female birds). Each of the samples obtained from bootstrapping (10x 3) were analysed by FISAT: the calculated mean male and female wing lengths and counts of frequency of each sex in the sample were compared to the values from the known sex data. To test whether FISAT performed as accurately for samples containing both similar and uneven numbers of male and female birds, five of each of the ten samples had equal numbers of male and female birds and five of the ten had one third female, two thirds male birds. Means of the mean wing lengths were then calculated for each sample size and results calculated using FISAT were tested against those calculated directly from the samples.

Paired t-tests showed no significant difference between the means of male and female wing lengths calculated using FISAT and the means calculated directly from the different sized samples of known sex birds (sample size 60: $t_{19} = 0.619$, $P > 0.05$; sample size 80: $t_{19} = 0.935$, $P > 0.05$; sample size 100: $t_{19} = 0.099$, $P > 0.05$). However the value of t reduced with a sample size of 100 suggesting that increased sample size improved confidence in results. When samples contained unequal numbers of male and female birds there was greater scatter in the FISAT results (figure 18); to have confidence of mean wing lengths calculated using FISAT being within 0.3mm of actual mean wing lengths of females and counts calculated using FISAT being within 3 of the actual female population sample sizes of 100 birds are needed. For males sample size of 100 birds gave confidence in FISAT results of being within 0.2mm of actual mean wing lengths (with the exception of one outlier) with confidence in counts being as for females. Male results were probably slightly better than those for females because there were more males in half of the samples. Sample sizes of 100 produced results clustered closer to the origin than the smaller samples with samples of 60 and 80 producing one outlying result in every 10 results for both male and female mean wing length or count (figure 18). Therefore, for this project, minimum sample sizes of 100 birds were used for analysis using FISAT wherever there was

sufficient data to do so. For some years, at some sites, data had to be grouped across years to achieve this sample size.

(a) Females



b) Males

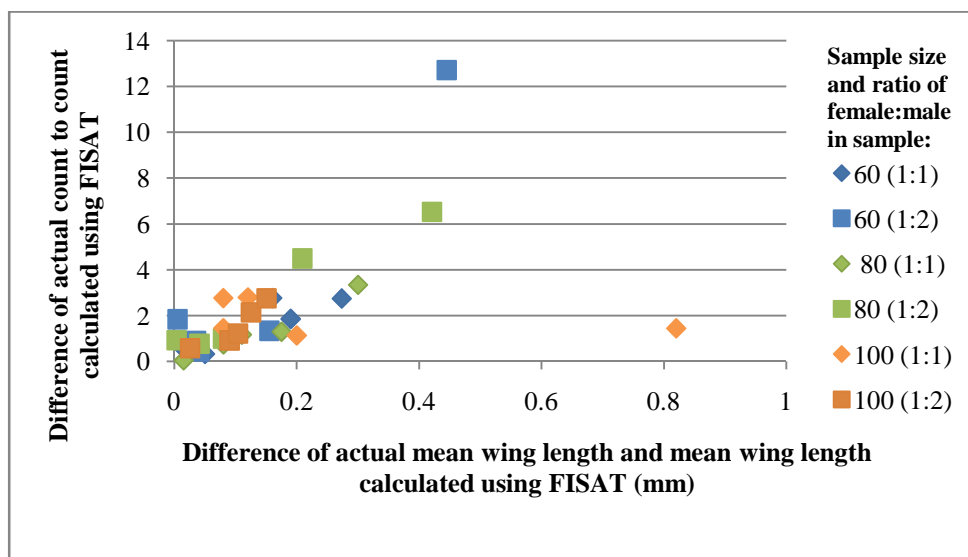


Figure 18. Differences in mean wing lengths (mm) and count of (a) female and (b) male Willow Warblers calculated directly (with birds' sex identified by presence of sexual characteristic) and calculated using FISAT software (from data of Willow Warblers caught at Wicken Fen, 1990-2009). Results are shown for ten of each sample size, 60, 80 and 100 birds, with the proportion of male and female birds in the sample (five of each sample had equal numbers of males and females, five of each sample had one third females, two thirds males).

The BTO holds data for nearly 30,000 Willow Warblers caught since 1990, of which only 7930 have been sexed by sexual characteristics. At Wicken Fen only 1931 females and 1551 males have been identified by sexual characteristics, out of 14184 birds caught April-June, 1968-2008. The value of using FISAT, even though, to ensure accuracy of results, it requires larger samples of birds than samples of birds of known sex, is that results of over 22,000 more birds are able to be included in the analysis. Critically, it enables data from earlier years to be included, when otherwise sample sizes would be too small for sufficiently accurate analysis.

Statistical techniques

I tested differences in mean wing lengths between sites using single factor ANOVA and tested variances found with a Tukey test. I tested the significance of differences in mean wing lengths between two sites for the same year/group of years using paired t-tests. I tested the significance of changes in mean wing lengths with time using regression analysis. Pearson's product-moment correlation (r) was used to test significance of correlations (Fowler & Cohen). In all tests two tailed significance $P < 0.05$ was used as the level for significance, with the null hypothesis that there would be no change with time or no difference in length between samples of mean wing lengths. Values of $0.1 > P > 0.05$ are reported as having a tendency for significance and for these the value of P is reported.

Presentation of data

Trend lines show best fit regression lines and error bars indicate $\pm 95\%$ confidence for graphs reporting changes in mean wing lengths and \pm standard error for correlations. For regressions the number of birds in samples being analysed are reported as $n =$ (sample size). Horizontal arrows indicate where years have been grouped to obtain sample sizes ≥ 100 . Tables of data held by the BTO and from individual sites are found in the appendix (tables 2-5).

Results

Data from the breeding and migration sites cover different time periods and vary in quantity; this affects the number of years for which data have to be grouped to enable the use of FISAT (figure 19).

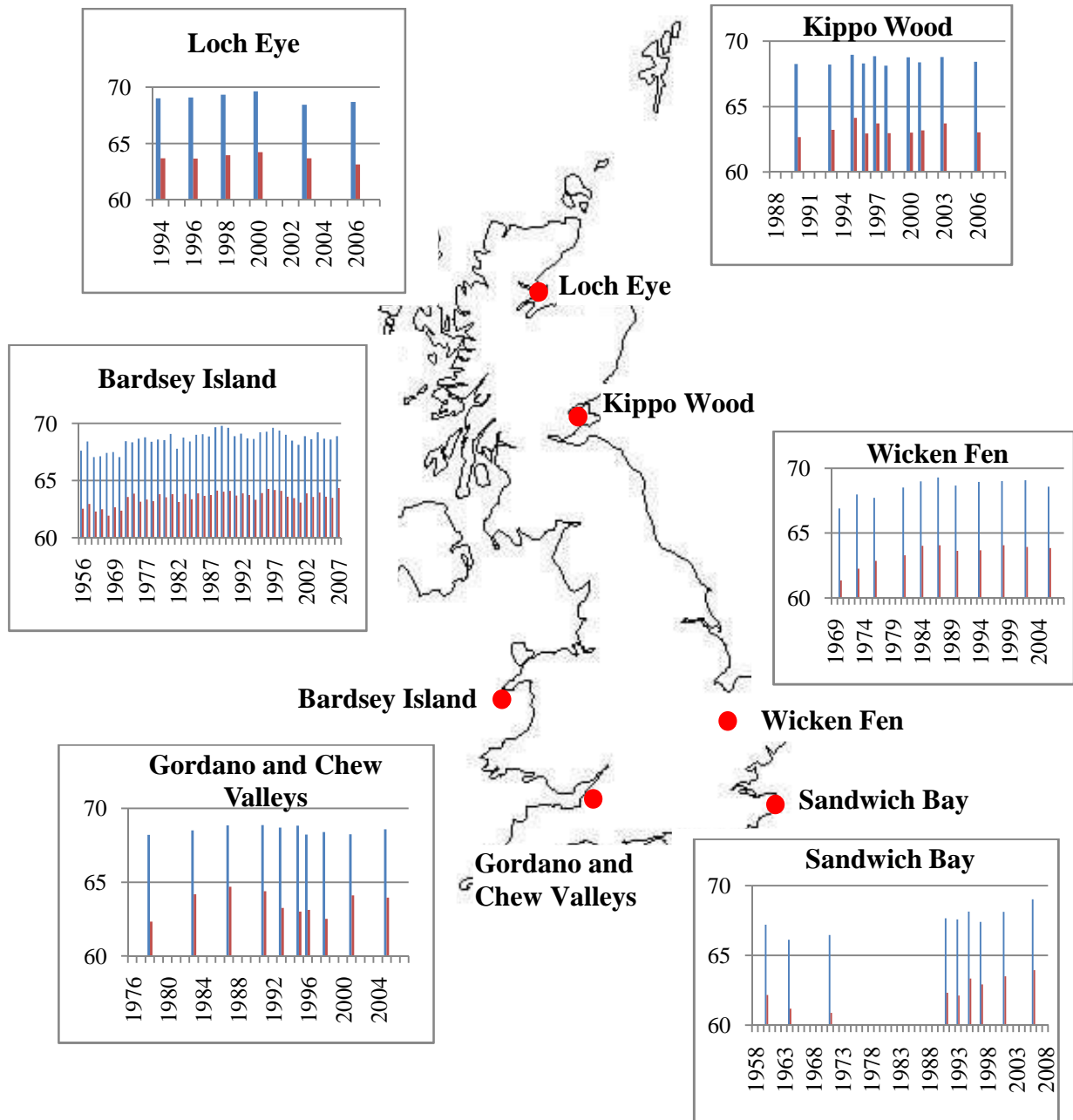


Figure 19. Locations of individual sites from which data was analysed, with graphs of mean wing lengths (mm) by year of adult male (blue) and female (red) Willow Warblers caught at each site. Where years have been grouped (to obtain sufficient numbers for analysing with FISAT) bars are in the middle year of the group.

Changes in mean wing length with latitude

The majority of Willow Warblers caught in Britain between April-June, 1967-2008, have been caught south of latitude 55° (approximately south of a line drawn between Newcastle and Carlisle) (figure 20). Indeed, there are only 2 records on the BTO database of adult Willow Warblers caught north of latitude 55° before 1986.

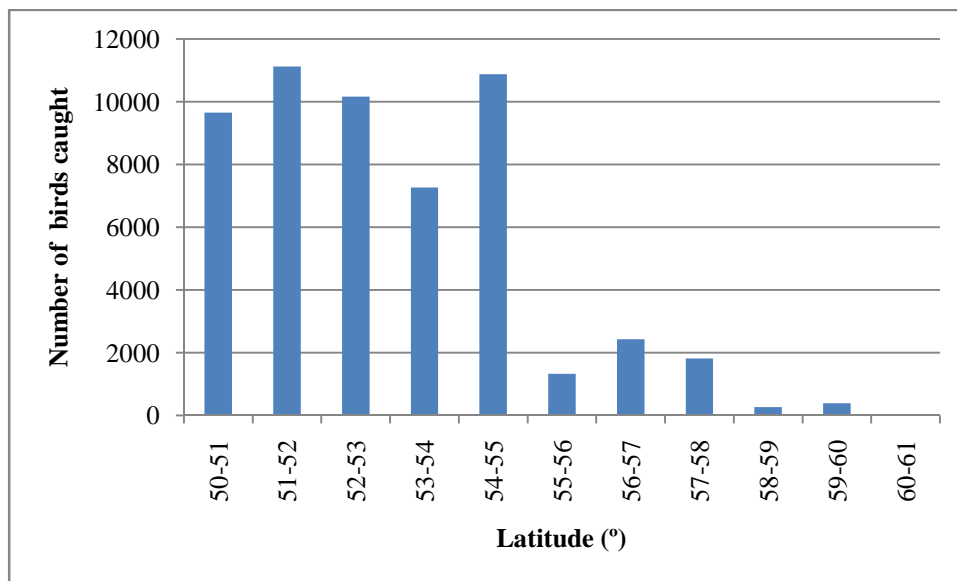


Figure 20. Number of adult Willow Warblers caught at different latitudes(°) between April-June in Britain, 1967-2008.

There was no significant change with latitude in mean wing lengths of male ($r^2=0.0692$, $df=8$, $P>0.05$, $n=25,535$) or female ($r^2=0.2184$, $df=8$, $P>0.05$, $n=25,788$) adult Willow Warblers, caught April to June, 1967-2008 (figure 21).

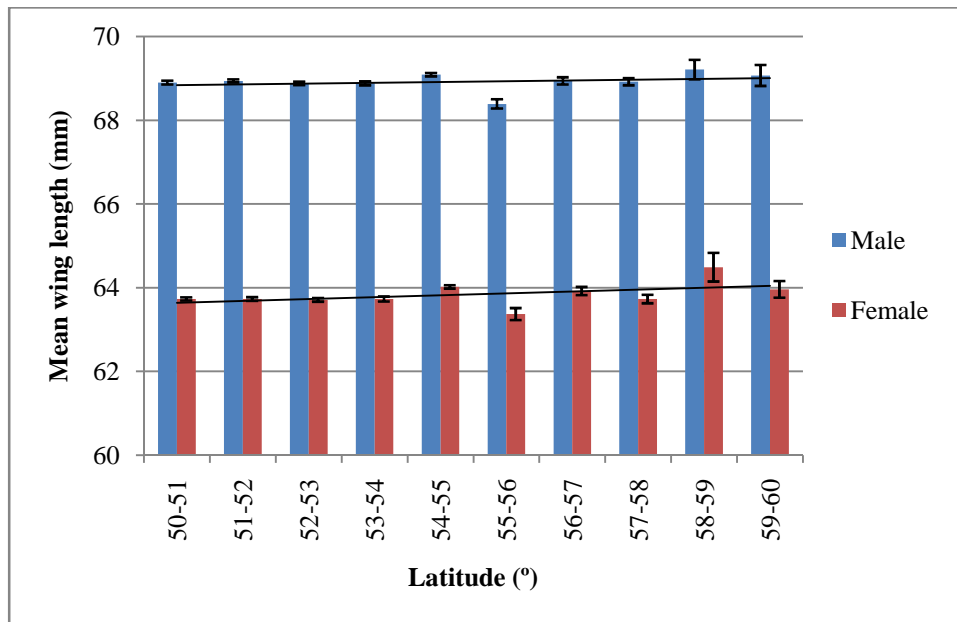


Figure 21. Mean wing lengths (mm) of adult Willow Warblers caught at different latitudes (°) in Britain between April-June, 1967-2008, shown with $\pm 95\%$ confidence intervals.

Comparison of mean wing lengths at breeding sites

While mean wing lengths of adult Willow Warblers show no significant difference when grouped by latitude, there are significant differences between male mean wing lengths of birds caught at the four breeding sites, 1994-2007 ($F_{3,12}=9.570$, $P<0.05$). Further analysis with a Tukey test showed that there were significant differences in male mean wing lengths between all but Kippo Wood and Chew Valley, and Loch Eye and Wicken Fen ($t_{4,12}= 0.451$, $P<0.05$) (table 2). There were no significant differences between female wing lengths at the different sites ($F_{3,12}= 2.452$, $P>0.05$). To perform the single factor ANOVA number of year groups available to be tested was reduced to four because of the need to group years to obtain sample sizes of 100 in each year group, and to match groups of years across sites. This reduces confidence in the test. Therefore, despite the risk of Type 1 errors, further T-tests were performed to test for differences in mean wing lengths between individual sites.

Table 2. Results of (a) ANOVA and (b) Tukey tests comparing mean wing lengths of adult Willow Warblers caught at breeding sites between April-June, 1994-2007. To perform this analysis data across years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

(a)

SUMMARY						
<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>		
Wicken	4	276.27	69.0675	0.000492		
Kippo Wood	4	274.01	68.5025	0.089892		
Loch Eye	4	276.08	69.02	0.0722		
Chew & Gordano Valleys	4	273.76	68.44	0.0218		
ANOVA						
<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	1.32335	3	0.441117	9.569556	0.001663	3.490295
Within Groups	0.55315	12	0.046096			
Total	1.8765	15				

(b)

	Sample	Kippo Wood	Loch Eye	Chew and Gordano Valleys
Wicken	69.0675	0.565	0.0475	0.6275
Kippo Wood	68.5025		-0.5175	0.0625
Loch Eye	69.02			0.58
Chew and Gordano Valleys	68.44			

Paired t-tests showed there was no significant difference between mean wing lengths of adult Willow Warblers caught at Loch Eye and Kippo Wood, April – June, 1994-2007 (males: $t_5 = 1.72$, $P > 0.05$, $n = 6$; females: $t_5 = 1.05$, $P > 0.05$, $n = 6$). However, mean wing lengths of male and female adult Willow Warblers caught at Kippo Wood were significantly shorter than those caught at Wicken Fen (figure 22) as were mean wing lengths of male adult Willow Warblers caught at Chew and Gordano Valleys (Kippo Wood: males $t_5 = 4.62$, $P < 0.01$, $n = 6$, females $t_5 = 3.10$, $P < 0.05$, $n = 6$,

Chew and Gordano Valleys: males $t_8 = 2.514$, $P < 0.05$, $n = 9$; females $t_8 = 0.617$, $P > 0.05$, $n = 9$). Male mean wing lengths were on average 0.532mm shorter and female mean wing lengths 0.76mm shorter at Kippo Wood, and male mean wing lengths on average 0.31mm shorter at Chew and Gordano Valleys, than at Wicken.

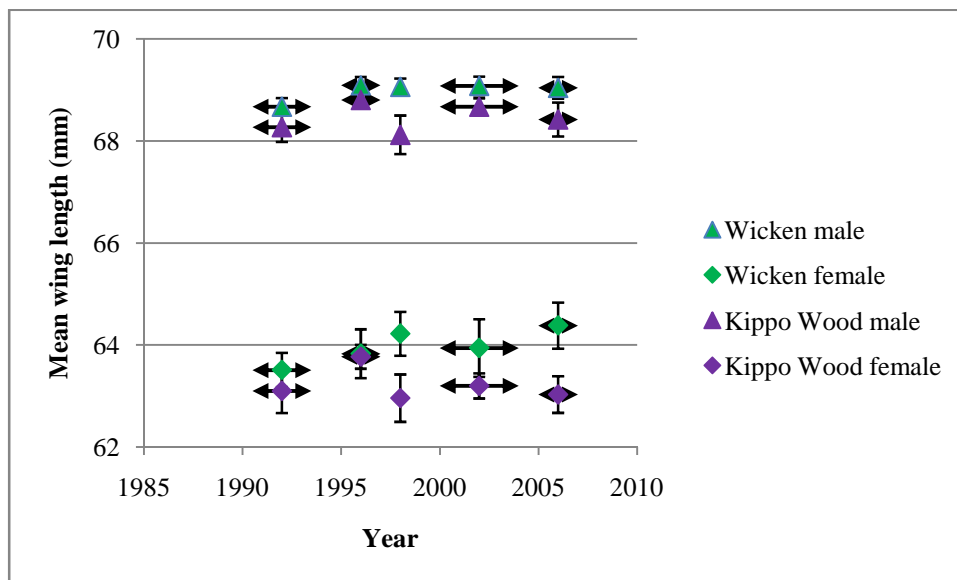


Figure 22. Comparison of mean wing lengths (mm) of male and female adult Willow Warblers caught at Wicken Fen and Kippo Wood, April-June, 1988-2007. Shown with $\pm 95\%$ confidence limits; horizontal arrows indicate where years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females, with Kippo Wood years grouped to match those required by Wicken Fen data.

A paired T test showed a significant difference between mean wing lengths of male Willow Warblers caught at Sandwich Bay and Bardsey Island for the years 1991-2007 ($t_5 = 2.97$, $P < 0.05$, $n = 6$), with male Willow Warblers caught on Bardsey Island having a mean wing length 0.98mm longer than those caught at Sandwich Bay. The difference between mean wing lengths of female Willow Warblers caught at Sandwich Bay and Bardsey Island in the same period tended towards significance ($t_5 = 2.422$, $P = 0.06$, $n = 6$) (figure 23).

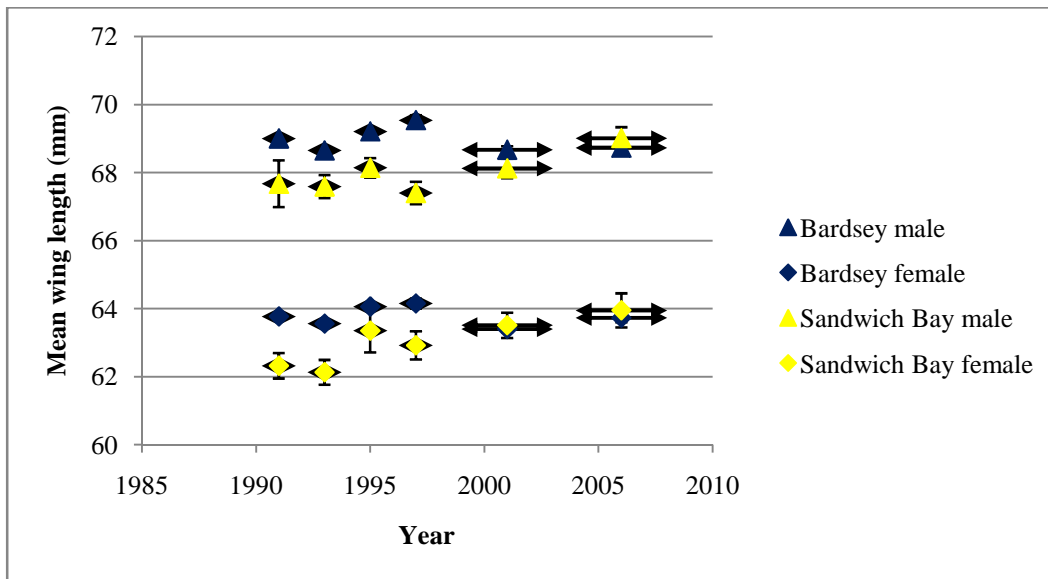


Figure 23. Mean wing lengths (mm) of male and female adult Willow Warblers caught at Bardsey Island and Sandwich Bay on spring migration, 1991-2008. Shown with $\pm 95\%$ confidence limits, horizontal arrows indicate where years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

Changes in mean wing length with time

Analysis of data from across Britain

Between 1967-1985 there was a significant increase in mean wing lengths of adult male (mean wing (mm) = $-80.719 + 0.076 \text{ year}$; $r^2=0.592$, $P<0.01$, $n=1390$) and female (mean wing (mm) = $-140.61 + 0.103 \text{ year}$; $r^2=0.468$, $P<0.05$, $n=856$) Willow Warblers, caught in the breeding period, April-June, in Britain. This was followed by a significant decrease in male (mean wing (mm) = $101.32 + -0.016 \text{ year}$, $r^2= 0.188$, $P<0.05$, $n=23$, $n=28,497$) and female (mean wing (mm) = $124.66 + -0.030 \text{ year}$, $r^2=0.322$, $P<0.01$, $n=25,312$) mean wing lengths for the period 1986-2008 (figure 24).

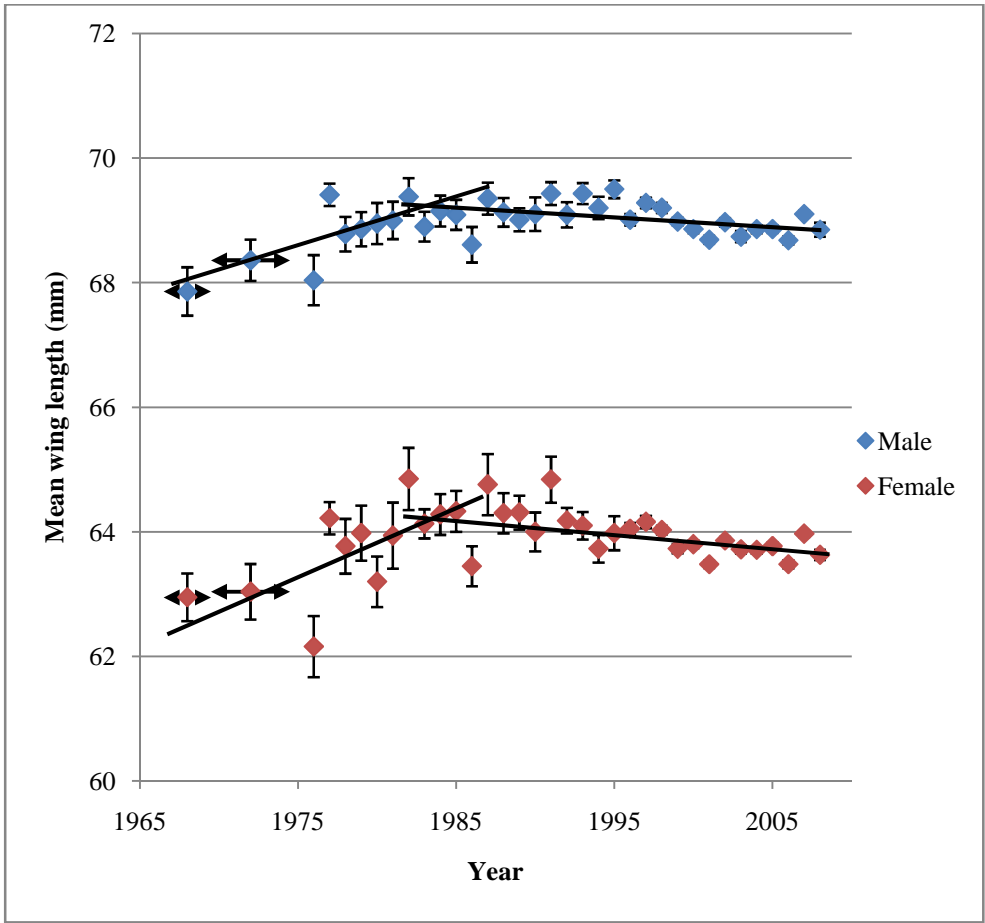


Figure 24. Mean wing lengths (mm) of male and female adult Willow Warblers caught in April-June in Britain. Shown with $\pm 95\%$ confidence limits; best fit regression lines are shown for years 1967-1985 and 1986-2008; horizontal arrows indicate where years were grouped to obtain sufficient sample sizes to use FISAT to calculate separate mean wing lengths for males and females.

For the periods, 1967-1985 and 1986-2008, there was no significant change in distribution of catch of Willow Warblers by month ($t_2 = 2.147$, $P > 0.1$; 1967-85 $n = 2,246$, 1986-2007 $n = 53,809$) so an increase in abrasion of primary feathers is not likely to be a confounding factor (figure 25).

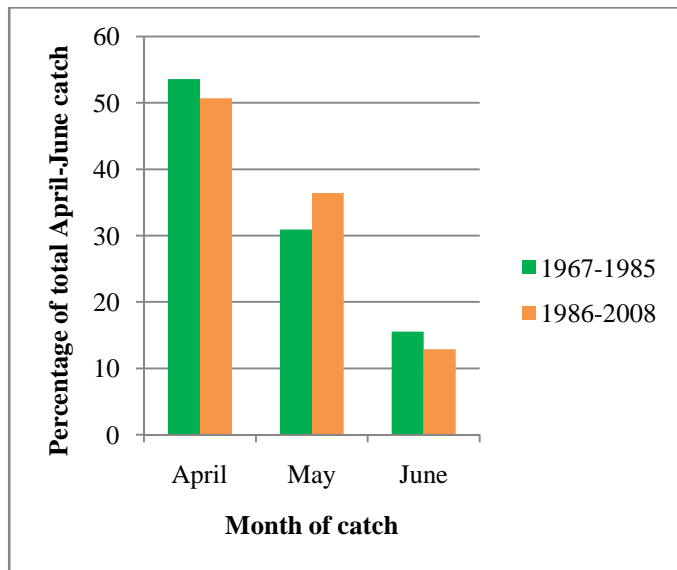
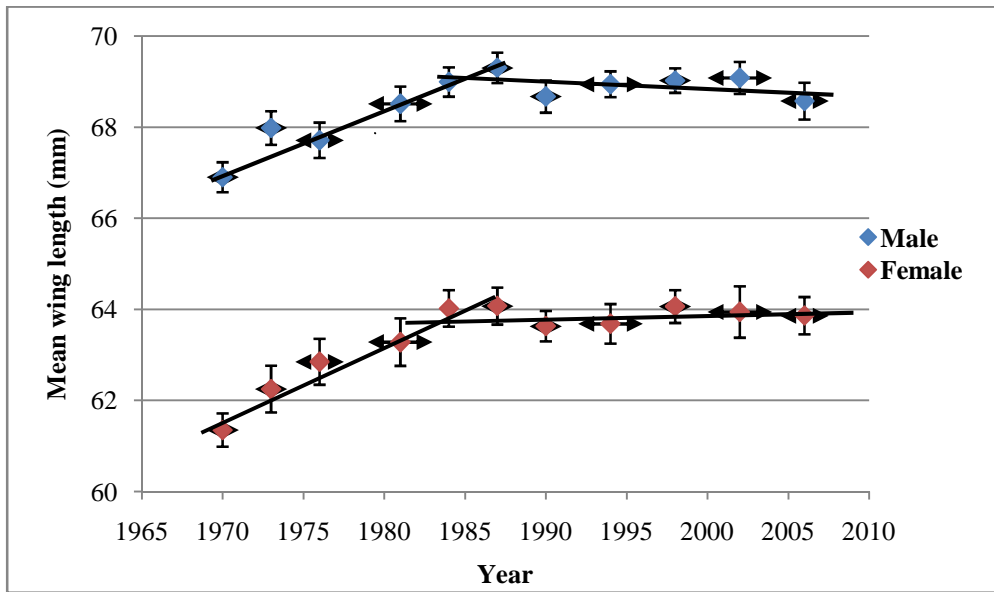


Figure 25. Percentage of adult Willow Warblers caught each month, April to June, of the total catch of Willow Warblers for the years 1967-1985 and 1986-2008.

Changes in mean wing lengths with time at breeding sites

Wicken Fen, and Chew and Gordano Valleys, are the only breeding sites with data from before 1985. At both sites there were increases in mean wing lengths of male and female adult Willow Warblers in the period up to 1985, however there is only sufficient data from Wicken Fen to show that the increases are significant for both males (mean wing (mm) = $-189.78 + 0.130 \text{ year}$, $r^2=0.878$, $P<0.05$, $n=418$) and females (mean wing (mm) = $-280.47 + 0.174 \text{ year}$, $r^2=0.959$, $P<0.01$, $n = 194$). Since 1985, at both sites (Wicken Fen 1986-2008, Chew and Gordano Valleys 1986-2007), there was no significant change in either male (Wicken Fen $r^2=0.195$, $P>0.05$, $n=447$; Chew and Gordano Valleys $r^2=0.372$, $P>0.05$, $n = 639$) or female (Wicken Fen $r^2=0.011$, $P>0.05$, $n= 257$; Chew and Gordano Valleys $r^2= 0.077$, $P>0.05$, $n= 448$) mean wing lengths (figure 26).

(a)



(b)

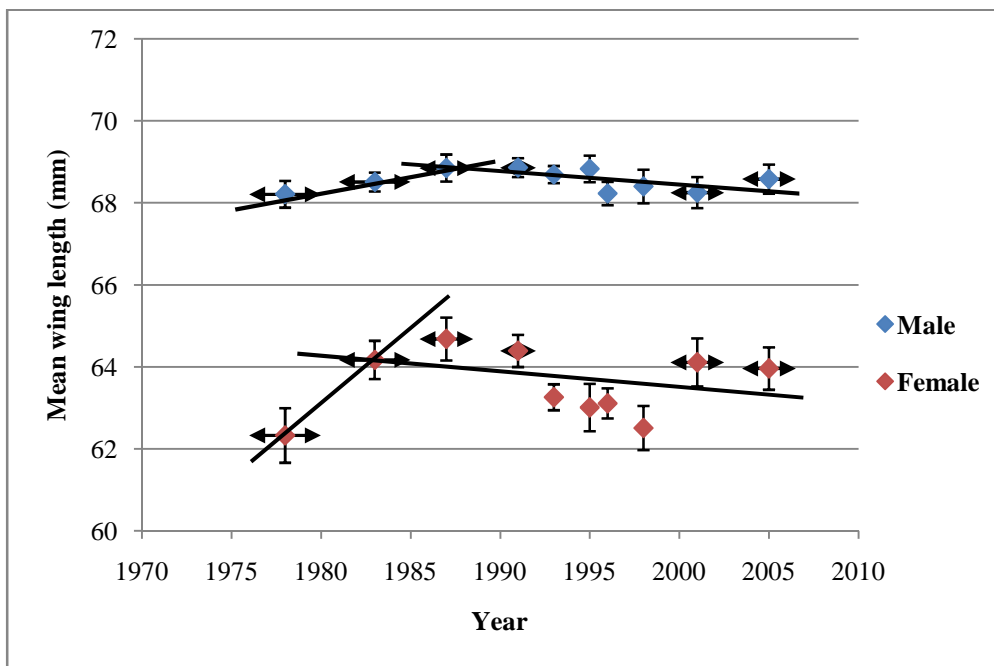


Figure 26. Mean wing lengths (mm) of male and female adult Willow Warblers caught April-June at (a) Wicken Fen, 1969-2008 and (b) Chew and Gordano Valleys, 1976-2007. Shown with $\pm 95\%$ confidence limits, and best-fit regression lines for years up to and including 1985 and 1986 on; horizontal arrows indicate where years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

The changes in mean wing length shown by Willow Warblers at Wicken Fen is not likely to be confounded by changes in abrasion (figure 27). Even in the period 2005-2008, when there was considerable increase in the proportion of birds caught in April, so reducing abrasion effect on wing length to the minimum, male wing lengths (the sex most caught in April) decreased. It is possible the decrease shown in mean wing length would have been greater if this effect had been allowed for.

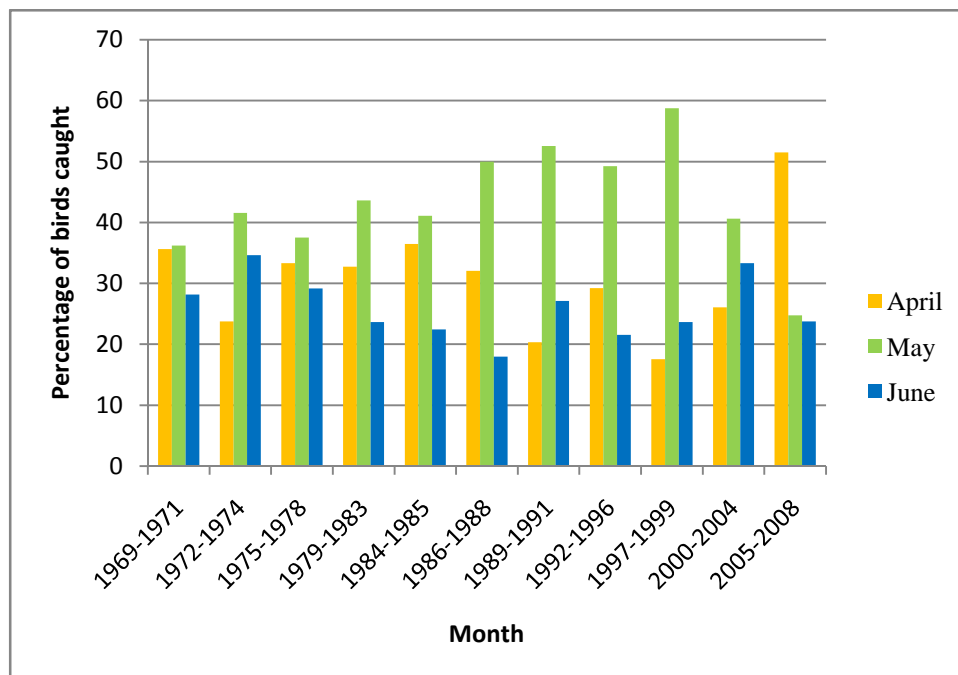
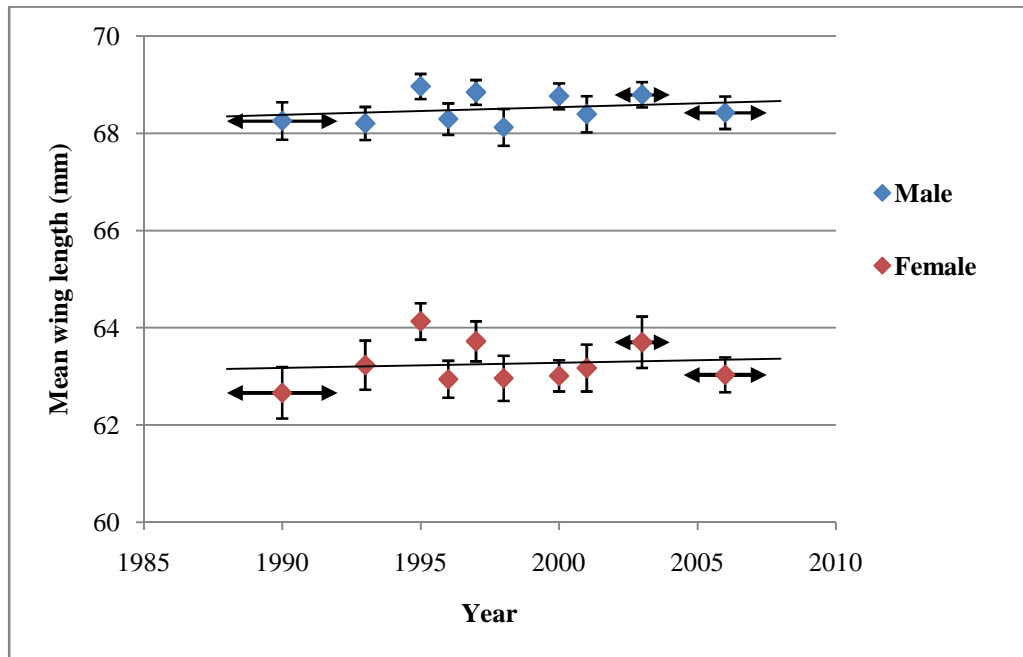


Figure 27. Proportion by month of adult Willow Warblers caught at Wicken Fen in the breeding period, April-June, calculated as a percentage of the total adult Willow Warbler catch for each group of years' breeding periods, 1969-2008.

At the two sites in northern Britain, Kippo Wood and Loch Eye, data is not available for the years before 1985. For the time frame from which data is available, mean wing lengths showed no significant change with time (Kippo Wood male mean wing: $r^2=0.060$, $P>0.05$, $n=1011$; female mean wing: $r^2=0.012$, $P>0.05$, $n=561$; Loch Eye male mean wing: $r^2=0.219$, $P>0.05$, $n=416$; female mean wing: $r^2=0.185$, $P>0.05$, $n=219$) (figure 28).

(a) Kippo Wood



(b) Loch Eye

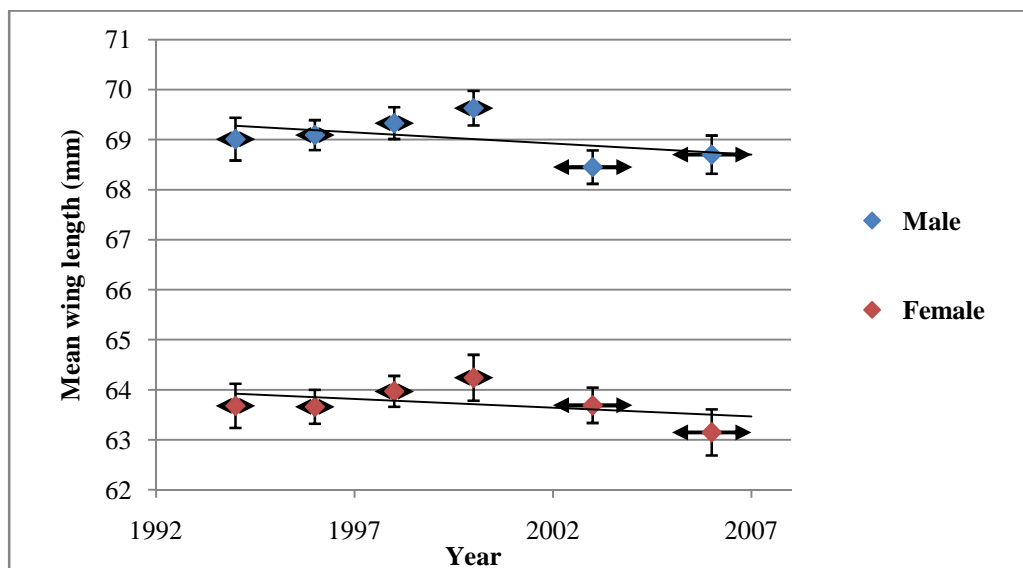


Figure 28. Mean wing lengths (mm) of male and female adult Willow Warblers caught in April – June at (a) Kippo Wood, 1988-2008 and (b) Loch Eye, 1994-2007. Shown with \pm 95% confidence limits, and best –fit regression lines; horizontal arrows indicate where years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

Changes in mean wing length with time at migration sites in spring

Changes in male and female mean wing lengths by week during spring migration of Willow Warblers caught at Bardsey Island (males $r^2 = 0.084$, $P > 0.05$, $n = 7,740$; females $r^2 = 0.366$, $P = 0.064$, $n = 11,761$) and Sandwich Bay (males $r^2 = 0.004$, $P > 0.05$, $n = 695$; females $r^2 = 0.145$, $P > 0.05$, $n = 568$) are not significant and therefore changes in timing of ringing effort in different years should not confound results.

Changes in mean wing lengths of Willow Warblers caught on spring passage on Bardsey Island show similar trends to those caught at Wicken Fen and Chew and Gordano Valleys. Mean wing lengths of male (mean wing (mm) = $-26.985 + 0.048 \text{ year}$, $r^2 = 0.383$, $P < 0.01$, $n = 7932$) and female (mean wing (mm) = $-36.941 + 0.051 \text{ year}$, $r^2 = 0.515$, $P < 0.01$, $n = 11,570$) Willow Warblers caught in the period 1956-1985, showed a highly significant increase. After 1985 male mean wing lengths showed a significant decrease (mean wing (mm) = $130.21 - 0.031 \text{ year}$, $r^2 = 0.217$, $P < 0.05$, $n = 5,360$) but the decrease in female mean wing lengths was not significant ($r^2 = 0.021$, $P > 0.05$, $n = 7875$) (figure 29).

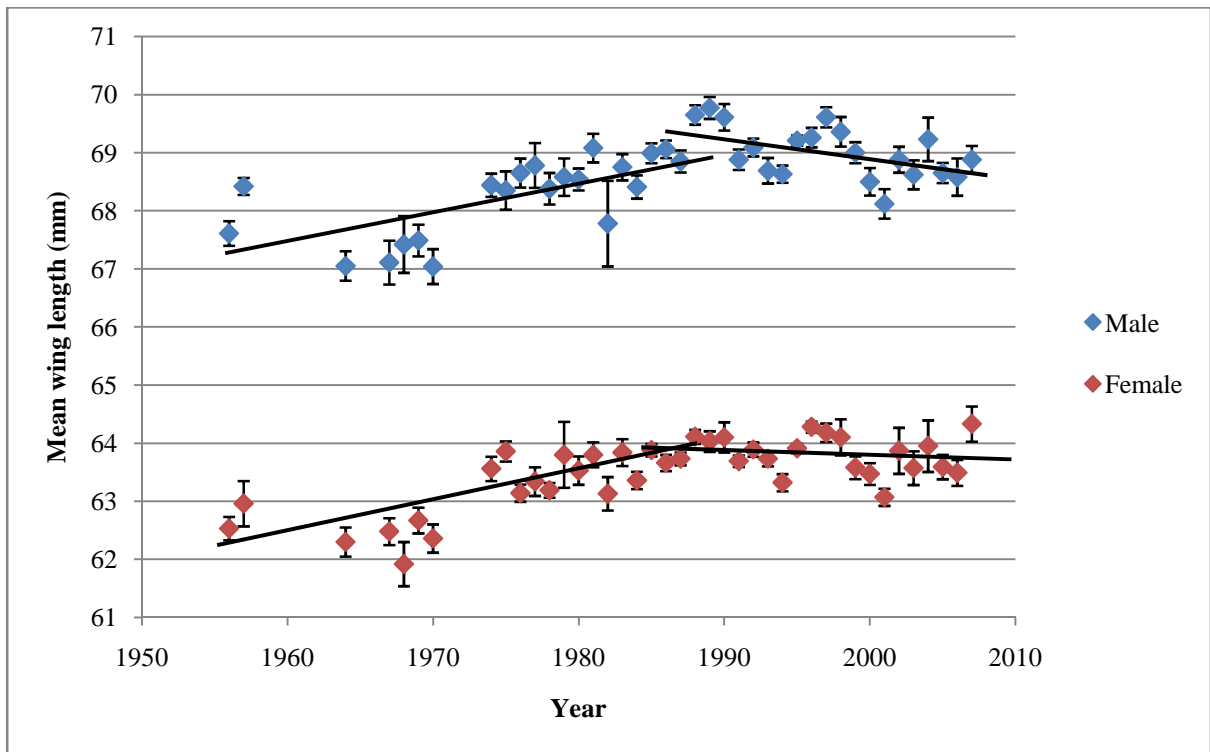


Figure 29. Mean wing lengths (mm) of male and female adult Willow Warblers caught on spring migration on Bardsey Island, 1956-2007. Shown with $\pm 95\%$ confidence intervals; best-fit regression lines are drawn for the periods 1956-1985 and 1986-2007.

Data from Sandwich Bay is not available for the key years for this project of 1970-1989. However, for 1991-2008, unlike the trends of no change or decrease in mean wing lengths shown in data from Britain analysed as a whole and by individual site, female mean wing lengths showed a significant increase with year (mean wing (mm) = $-164.61 + 0.114 \text{ year}$, $r^2=0.793$, $P<0.05$, $n= 321$), and male mean wing lengths showed a tendency to increase (mean wing (mm) = $-100.87 + 0.085 \text{ year}$, $r^2=0.646$, $P = 0.063$, $n=389$) (figure 30).

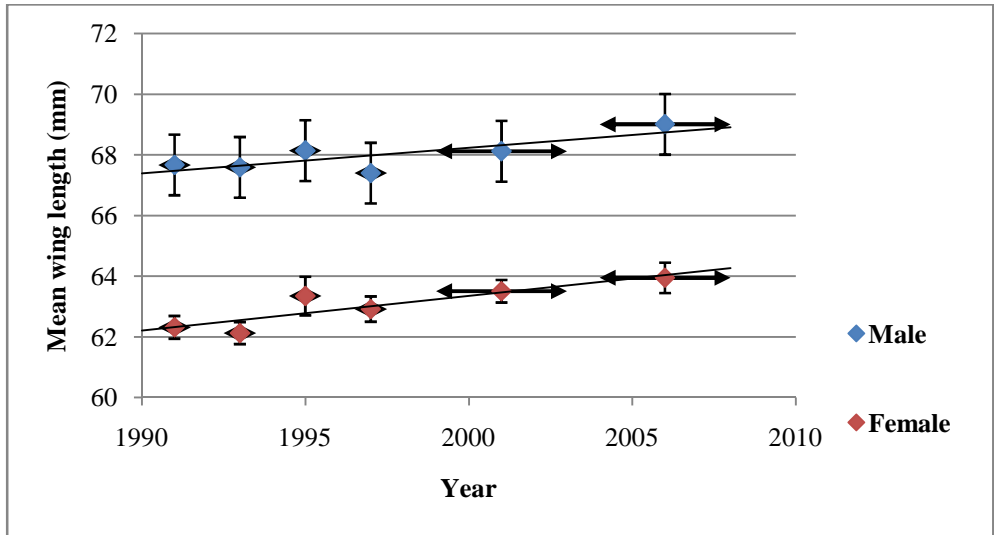


Figure 30. Mean wing lengths (mm) of male and female Willow Warblers caught on spring migration at Sandwich Bay, 1991-2007. Shown with $\pm 95\%$ confidence limits, and best-fit regression lines; horizontal arrows indicate where years have been grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

Of the sites included in this study, Wicken Fen and Bardsey Island provide the longest continuous datasets. A paired t-test showed no significant difference between mean wing lengths of male and female Willow Warblers caught at these two sites between 1969-2008 ($t_{10} = 1.389$, $P > 0.05$, $n = 12$). This is particularly striking as at both sites Willow Warblers' data showed significant changes in mean wing length with time and one is a site where birds are caught on migration and one a breeding site (figure 31).

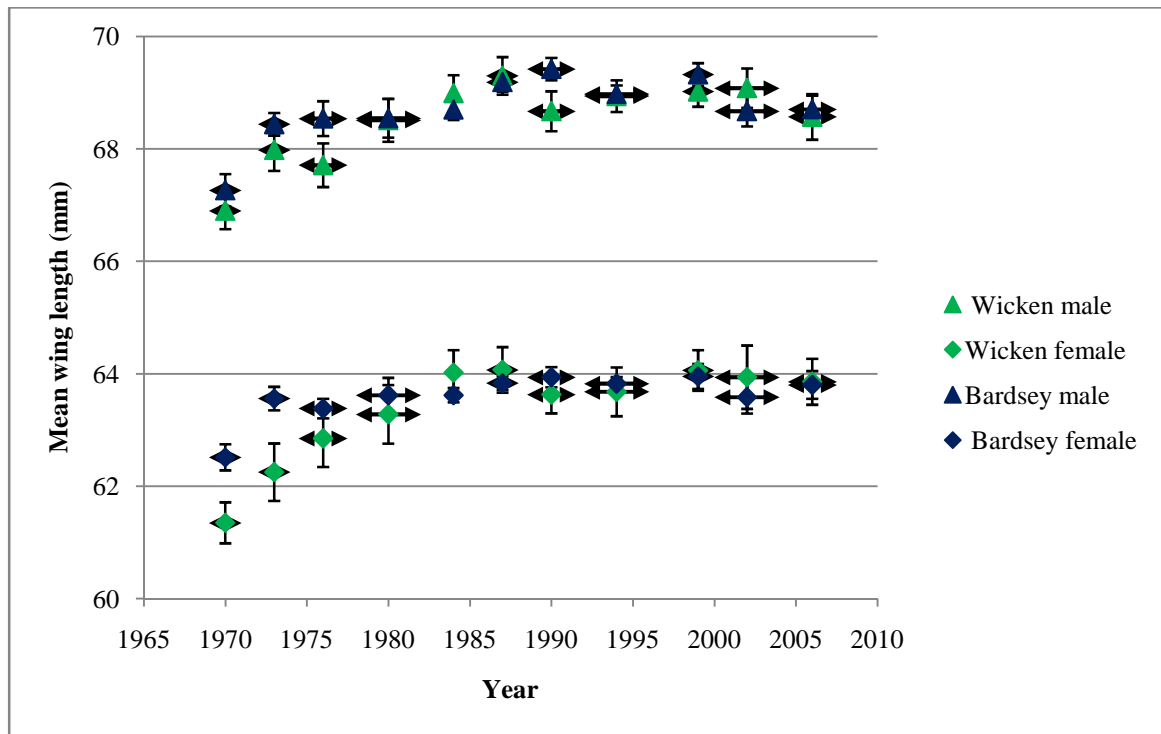


Figure 31. Mean wing lengths (mm) of male and female adult Willow Warblers caught at Wicken Fen and Bardsey Island, 1969-2008. Shown with $\pm 95\%$ confidence limits, horizontal arrows indicate where years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females, with Bardsey years grouped to match those required by Wicken Fen data.

Correlation of male and female mean wing lengths

There was a highly significant correlation between mean wing lengths of adult male and female Willow Warblers caught April-June, 1976-2008 (years for which there are sufficient records to enable use of FISAT without grouping years together) in Britain ($r_{31}=0.837$, $P<0.01$, $n=33$) (figure 32). As mean wing lengths of females increased or decreased so did males. This suggests that both sexes are affected similarly by any drivers to changes in mean wing length.

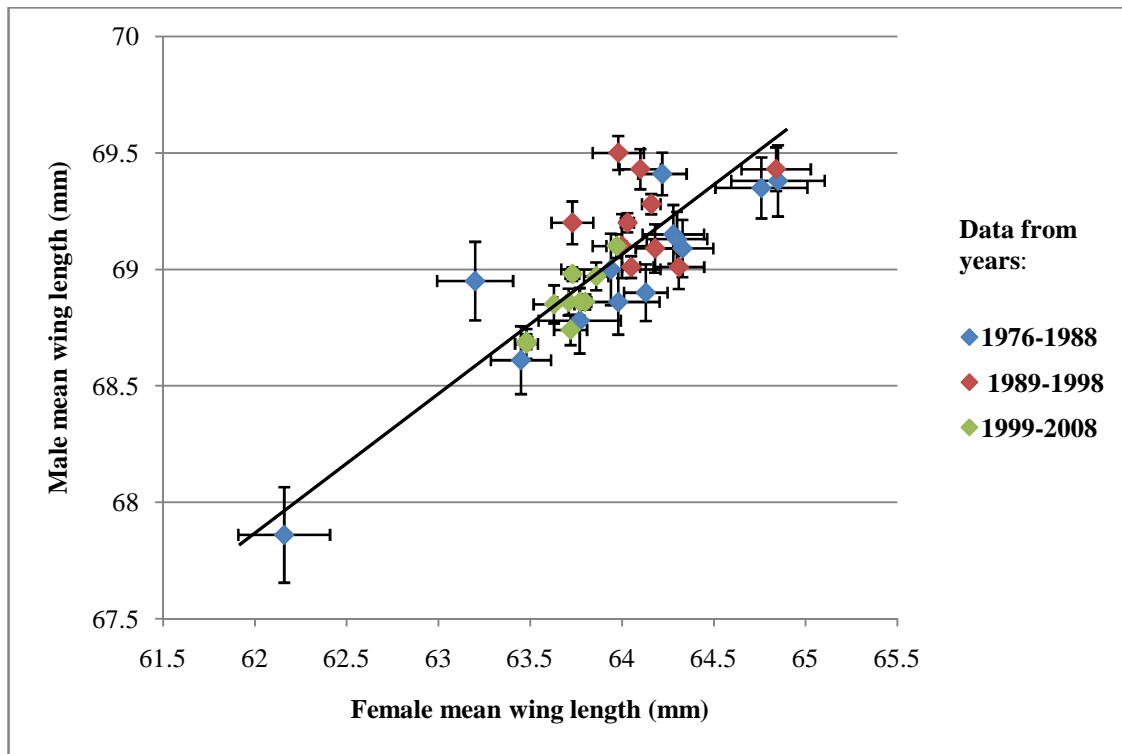
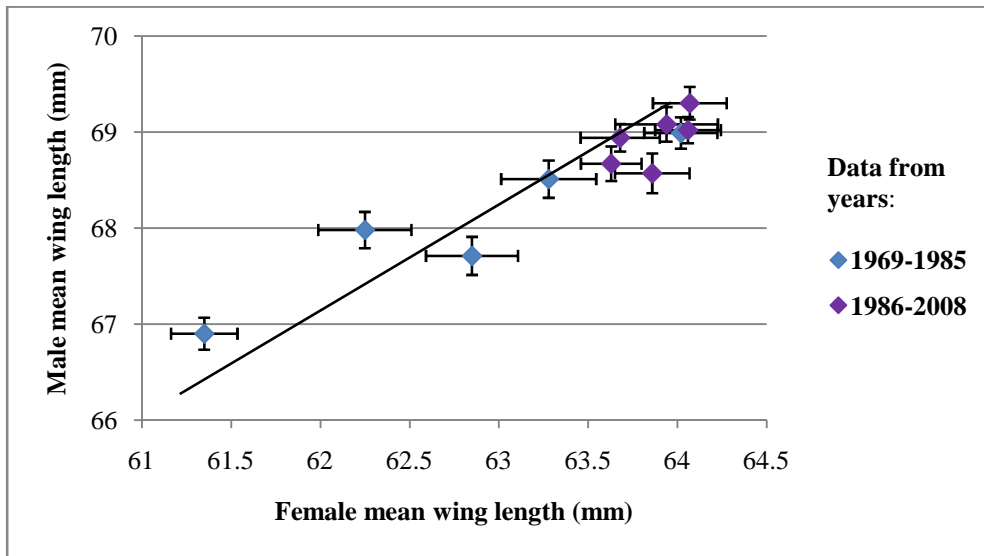


Figure 32. Correlation of male and female adult Willow Warblers' mean wing lengths (mm), caught April – June, 1976-2008, in Britain. Shown with \pm standard errors and best fit trend line.

This highly significant correlation of mean wing lengths of male and female Willow Warblers is also found at two of the individual breeding sites, Wicken Fen ($r^2=0.904$, $r_9=0.951$, $P<0.01$, $n=11$) and Kippo Wood ($r^2 = 0.633$, $r_8=0.796$, $P<0.01$, $n=10$) (figure 33) but not at Loch Eye ($r^2=0.583$, $r_4=0.763$, $P>0.05$, $n=6$) or Chew and Gordano Valleys ($r^2= 0.239$, $r_8=0.49$, $n=10$). At Wicken Fen and Kippo Wood, as female mean wing lengths increased or decreased so did male mean wing lengths. That they are highly correlated at individual site level suggests that at these sites both sexes are affected by the same drivers to changes in mean wing length.

(a)



(b)

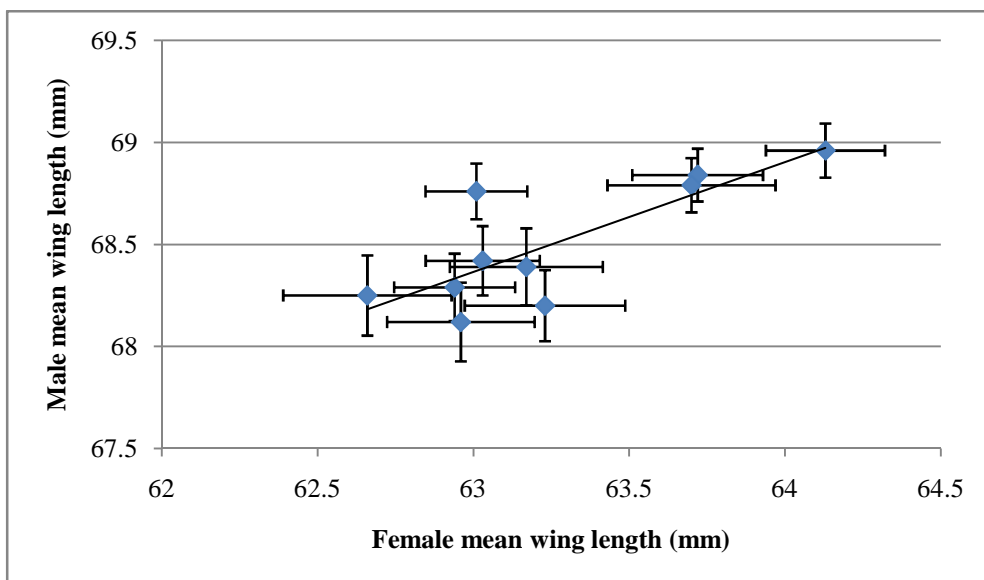
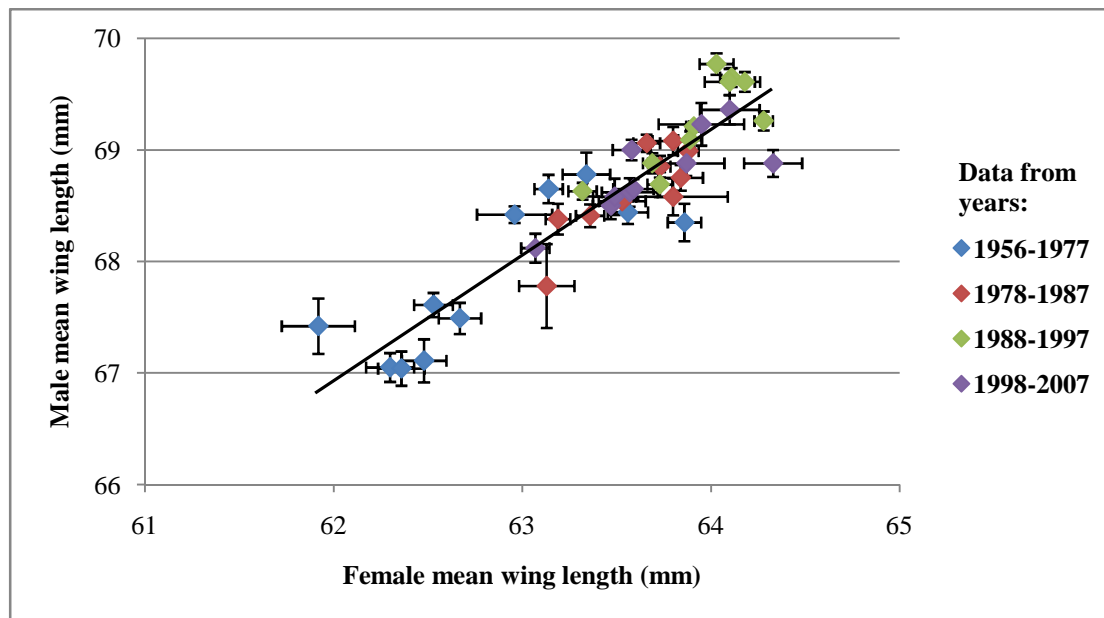


Figure 33. Correlation of mean wing lengths (mm) of adult male and female Willow Warblers caught April-June at (a) Wicken Fen, 1969-2008 (b) Kippo Wood 1988-2008. Shown with \pm standard errors; where necessary years were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

At the two sites where Willow Warblers are caught on migration, male and female mean wing lengths were highly significantly correlated (Bardsey Island: $r_{39} = 0.907$, $P < 0.01$, $n = 41$; Sandwich Bay: $r_7 = 0.937$, $P < 0.01$, $n = 9$) (figure 34). The strength of this correlation is particularly striking as at these

sites the majority of males are caught at a different time to the females. This further supports the possibility that male and female Willow Warbler populations are affected by the same drivers to change in wing length.

(a)



(b)

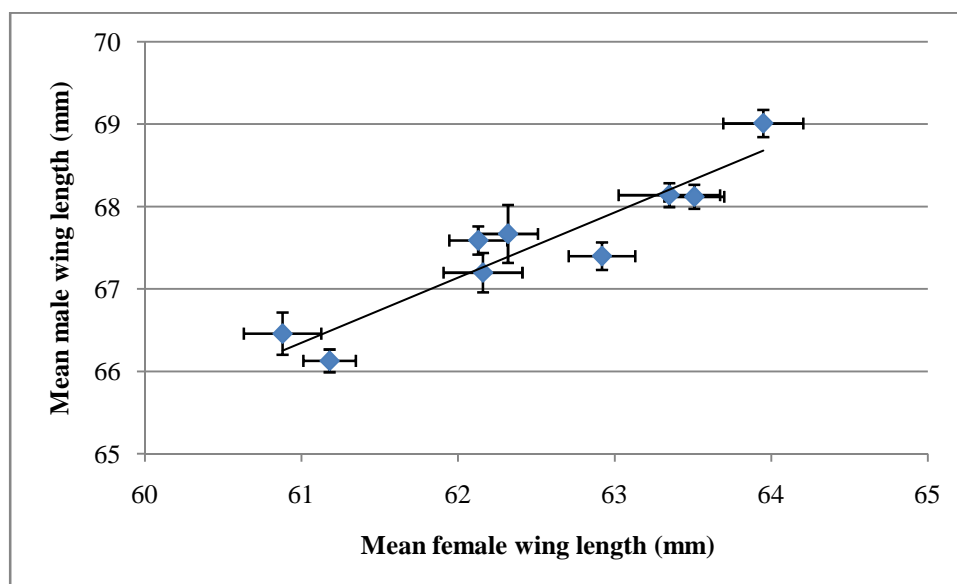


Figure 34. Correlation of mean wing lengths (mm) of male and female Willow Warblers caught on spring migration at (a) Bardsey Island, 1956-2007 and (b) Sandwich Bay, 1958-2008. Shown with \pm standard errors; where necessary data from Sandwich Bay were grouped to have sufficient sample sizes to enable use of FISAT to calculate separate mean wing lengths for males and females.

Discussion

Changes in mean wing lengths with latitude

Analysis of data from all adult Willow Warblers caught in Britain showed no significant changes in male or female mean wing lengths with increased latitude. There were significant differences between mean wing lengths of male birds caught at individual breeding sites but these were not consistent with changes in latitude, for example mean wing lengths were longer at Wicken Fen than at Kippo Wood, a northern site and Chew and Gordano Valleys, a southern site. The strength of results of comparisons of mean wing lengths between individual breeding sites is limited by variations in the quantity and temporal distribution of their data, particularly from the northern sites. This is illustrated by the differences in results produced using the Tukey test and paired t-tests; results of the latter are supported by a visual inspection of the relevant graphs and therefore unlikely to be a construct of a Type 1 error (figure 22). Overall, this study provides no evidence for the presence of sub-species of Willow Warblers at different latitudes in Britain, unlike in Sweden where there is clear evidence for a migratory divide (Bensch 2009). As in both glacial and recent history there have been no geoclimatic features in Britain that would isolate populations of Willow Warblers this finding is not surprising.

Relationship of changes in wing length changes with changes in abundance

The prediction that changes in mean wing length would occur with changes in abundance, the latter reflecting changes in stresses on Willow Warbler populations, broadly held at the two breeding sites with data covering the relevant period, Wicken Fen and Chew and Gordano Valleys and at one of the two migration sites studied, Bardsey Island. Similar trends, with changes in wing length occurring either side of the 1985 peak of abundance, were also shown in the analysis of data from the total data set of all Willow Warblers caught in Britain between April and June. For the sites with data available

only after 1985, results in the relevant period are the same as for those sites with longer data sets, i.e. showing no significant change in mean wing length after 1985. As patterns of change in wing lengths are similar at all the sites studied, with the exception of Sandwich Bay, it is likely that the same factors are driving the changes in wing length in Willow Warbler populations breeding in Britain. Establishing how far this potential correlation of changes in mean wing length with changes in abundance is causal will be difficult, as it could be driven by pressures on the birds at their wintering or breeding grounds. However, as changes in mean wing lengths are similar between northern and southern Britain and trends in abundance differ, it is likely that the cause(s) of changes in abundance are different, or additional to, those causing the changes in mean wing lengths.

These results differ from those of Yom-Tov *et al.* (2006b) who found a linear decrease in residual wing length of Willow Warblers at Wicken Fen for the whole period studied for this project. However his sample size ($n=331$), just under 10 records a year, was smaller than that used for this project ($n=1316$) and considerably smaller than the size of samples that I found necessary to avoid confounding of data.

There was no significant difference in mean wing lengths of Willow Warblers caught at Wicken Fen and Bardsey Island. This is particularly striking, given the different geographical location and the different use of the sites, one for breeding, the other a migration staging post and suggests the trends in wing lengths shown in the data analysed for this project are robust.

While the two northern sites studied showed similar trends for the rest of Britain for the period post 1985, further data is needed to explore whether this similarity is also found in the pre-1985 period. This would be particularly useful to explore given the different trends in abundance of northern and southern Willow Warbler populations.

Sandwich Bay is the only site where Willow Warblers showed a significant increase in mean wing lengths after 1985. It would be useful to compare this data with those from other southern coastal

migratory site to see if this trend continues to hold. However, the causes of this difference in trend may be difficult to determine. It would be possible that an increasing number of longer winged Continental Willow Warblers *P.t. acredula* are being caught here, although there is no evidence of this from ringing recoveries and there is no suggestion from the data that mean wing lengths of birds caught at Sandwich Bay, although increasing, are becoming longer than those caught elsewhere in Britain (figure 23).

Interestingly, the earliest data from Bardsey Island and Sandwich Bay, for the period 1956-1963, while too small a sample to be tested for significance, show a decrease in mean wing length. This raises the possibility of cyclical changes in mean wing lengths of Willow Warblers. However, there is no earlier data of population abundance to see this correlates with any changes in abundance.

Drivers of change in mean wing length are the same for both sexes

The high correlation shown between male and female mean wing lengths at four of the six sites studied, including the two sites where birds are caught on migration and in data of all Willow Warblers caught in Britain analysed as a whole, suggests that similar drivers of change are affecting male and female Willow Warblers. At Loch Eye results correlate except for one year and the small sample size probably confounds the result. At Chew and Gordano Valleys the strength of the correlation is affected by an unexplained decrease in female mean wing lengths in the mid-1990s.

Willow Warblers tend to be itinerant on their wintering grounds and travel further south as the season progresses, but little is known in detail about the locations or habitats of their wintering grounds. If their wing lengths had not remained correlated this would have raised the possibility that males and females experienced different conditions on their wintering grounds, putting different pressures on their populations. This study provides no support for this happening.

Changes in wing length with warmer temperatures

Allen's rule would predict an increasing wing length with increasing temperature and the increase in mean wing length, seen in the majority of data analysed for this project for the period before 1985, would conform to this rule (Millien *et al.* 2006). However, the stabilisation and decrease seen in mean wing length since 1985 would not be expected. If wing lengths had stabilised and not decreased it is possible that aerodynamic forces and allometric relationships with weight (Rayner 1988) were preventing further increases. The decrease since 1985 found in mean wing lengths in data of Willow Warblers in Britain analysed as a whole, and at some of the individual sites, is harder to explain. It could be a response to changes in climate conforming to Bergmann's rule: that body size decreases with increase in temperature. However, this process would have been expected to start prior to 1985. To understand better the effect of temperature on Willow Warblers' morphology, further study is needed that includes investigation into possible long-term changes in Willow Warblers' body size as well as wing length.

Changes in wing length with changes in habitat or predation pressures

Similar trends in changes in mean wing lengths are found at the sites with data sets that cover the pre1985 period and when the data for Britain is analysed as a whole. The habitats used by Willow Warblers at the individual sites studied are broadly similar, with Willow scrub being present at all. This suggests that change in habitats, at least at a broad scale, at breeding grounds is not a driver of the change in wing lengths. Searcy *et al.* (2004) found that early nutrition affected skeletal size of Song Sparrows *Melospiza melodia* that carried into adulthood. However, Song Sparrows are sedentary birds and it seems more likely that deficient nutrition would result in early mortality in long distance migrants, such as Willow Warblers, than these birds enter the adult population. Increase in predation pressure have been found to correlate with decreased body size and increased wing length of Great Tits (Gosler *et al.* 1995). However, at Wicken Fen, for example, predation pressure has increased since 1991 when both Marsh Harriers *Circus aeruginosus* and Sparrowhawks have bred at

the Fen and mean wing lengths of Willow Warblers have remained stable. It is possible that changes in wing lengths are responses to changes in habitat or predation pressures on migratory routes or wintering grounds, about which little is currently known.

Robustness of wing length measurements

This study was based on analysis of mean wing lengths. Andy Gosler is reported as suggesting there was a change in some ringers' wing measurement technique in the mid 1980s (Yom-Tov 2006b). However, Jacquie Clark, head of the BTO Ringing Unit, is not aware of any systematic change in wing length measurement technique over the period from which data has been used (pers. comm.). At Wicken Fen some of the same ringers, have been present since 1967, using the same measurement technique, (Chris Thorne, pers. comm.) and results are consistent with those from other sites elsewhere. The consistency of results from different sites across the country shown in this study encourages confidence in wing length as a measurement. In addition, at migration sites, visiting ringers are present for only part of a season (Steve Stansfield pers.comm) and hence each year a proportion of the males will have been measured by different ringers to those measuring the females. The high correlation of male and female mean wing lengths at Bardsey Island and Sandwich Bay sites suggests there is good consistency in measuring technique.

Suggestions for further work

This study would be improved by having more data from the pre-1985 period available for analysis. The records from Wicken Fen from 1968-1990 entered on computer for this project represent over a quarter of the 4789 computerised records currently (2008) held by the BTO for this period. The Bird Observatories Council's drive to computerise the data from observatories will be very helpful in this regard (Mark Grantham pers. comm.). Having more data from this earlier period would enable better understanding of changes at an individual site level and give greater confidence in results when analysed as a whole. In particular, further computerisation of early ringing data from northern Britain

is needed to explore any differences in changes in mean wing lengths over time between northern and southern populations.

It would be useful to study the relationship between changes in body size of Willow Warblers and their abundance using measures of weight (g) available in long term datasets. If a correlation was found, that might assist with understanding the drivers of changes in Willow Warblers' size. This was beyond the scope of this project as body weights are confounded by a number of factors, (such as time from sunrise of weighing, temperature over the previous 24 hour period; weather conditions; activity of the bird; and food availability) for which much detailed information is required.

Further work is needed to understand more closely the relationship of Willow Warblers' populations' changes in mean wing length with changes in abundance using more detailed information of changes in abundance provided by the BTO's Breeding Bird Survey and using measures of ringing effort at individual sites to calculate changes in Willow Warblers' abundance. However, the simplest measure of ringing effort, calculation of net feet hours, is confounded by changes in temperature and, especially across a long time period, of habitat. Data from the BTO's Constant Effort Sites, that attempt to control habitat and date of catching variables, will be useful, once they provide sufficiently long data sets to measure the long term changes involved, although more sites in northern Britain are needed. To understand whether changes in mean wing lengths of Willow Warblers is driven by a factor that is also acting on species, study of mean wing lengths of other trans-Saharan migrant species, such as Reed Warbler *Acrocephalus scirpaceus* (for which there are large datasets from Constant Effort Sites and for which there is evidence of fluctuations in abundance at least since 1980), would be useful as would comparisons with changes shown in sedentary species, such as Bullfinch *Pyrrhula pyrrhula*.

There is some suggestion that that there has been a decline in the population of female Willow Warblers present at Kippo Wood (James Cobb pers.comm). Study of the proportions of male and female Willow Warblers present at different sites over time might assist with understanding

populations' changes in abundance. In addition, it would be useful to investigate whether there have been changes in timing of arrival of males and females at migration and breeding sites to see whether changes in abundance are related to possible mis-timing of arrival and breeding with food availability as a result of climate change. This broad scale approach would support the more detailed but more limited evidence of any changes in timing of breeding available from nest records.

Wing length was first used as a measurement as it is easily and swiftly taken and was used to broadly separate species and sexes within species (Graham Martin pers.comm.). It would be useful to experiment with a different measure of size, for example tarsus length, to see if it has better repeatability than wing length measurement and if it provides sufficient information about individuals, for example their sex. At busy ringing periods, it would be difficult for ringers to take the time to add another measurement to those already being taken and an increase in processing time would be potentially detrimental to the birds. Therefore there would need to be considerable confidence in the efficacy and information derived from the new measurement for it to replace that of wing length, for which long datasets are available.

More needs to be known about Willow Warblers' wintering grounds and habitats as these may influence the changes seen in Britain in populations' mean wing length and abundance.

While this study suggests the same drivers are operating on male and female wing lengths, it is possible that different drivers are affecting their abundance. In addition, further study of wing lengths on Willow Warblers' wintering grounds would indicate whether there is a differential in distances travelled in Africa by males and females, as has been found, for example for Chiffchaffs (Catry *et al.* 2005), which then potentially experience different conditions with different impacts on their abundance.

Conclusion

The number of Willow Warblers breeding in Britain has declined since 1985 yet the cause(s) of this decline are not well understood. I have shown how simple analyses of count of wing length measurements give insights into male and female Willow Warblers' presence and activity at sites in Britain. I have found no evidence of changes in mean wing lengths with increased latitude, which would have given support to the presence of a migratory divide in the British breeding population. I have found that mean wing lengths of male and female populations breeding in Britain have changed over time, with changes timed with changes in abundance of populations. The strength of these trends and causes of these changes need further investigation. However, given the significant correlation of male and female wing lengths at the majority of the sites, and in BTO data as a whole, the factors driving changes in populations' male and female mean wing lengths are probably similar.

Acknowledgements

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Appendix

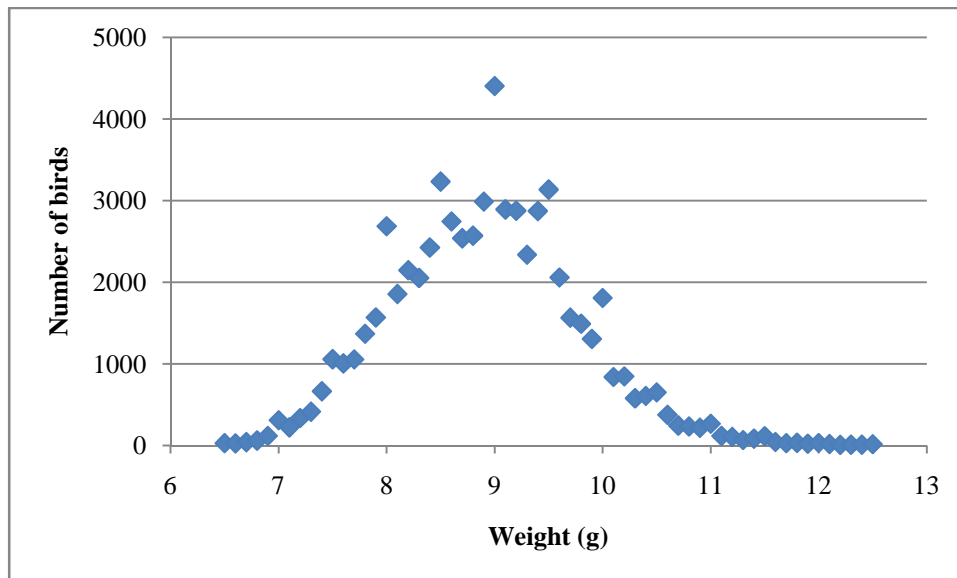


Figure 35. Weight (g) of adult Willow Warblers caught April-June in Britain, 1958-2008.

Table 3. Data from adult Willow Warblers, with records held by the BTO, caught in the period April-June, 1967-2008, with mean wing lengths (mm), standard errors and count of males and females. Data from individual birds are included once only in each year they are caught. Years are grouped where necessary to have sufficient data to enable use of FISAT to calculate male and female mean wing lengths and counts.

Year(s)	Males			Females			Total number of birds
	Mean wing length (mm)	Standard error	Number of birds	Mean wing length (mm)	Standard error	Number of birds	
1967-69	67.86	0.20	37	62.95	0.20	71	108
1970-75	68.36	0.17	78	63.04	0.23	67	145
1976	68.04	0.21	83	62.16	0.25	17	100
1977	69.41	0.09	265	64.22	0.13	151	416
1978	68.78	0.14	103	63.77	0.22	65	168
1979	68.86	0.14	126	63.98	0.23	52	178
1980	68.95	0.17	89	63.20	0.21	32	121
1981	69.00	0.15	105	63.94	0.27	49	154
1982	69.38	0.15	77	64.85	0.25	46	123
1983	68.90	0.12	162	64.13	0.12	107	269
1984	69.15	0.13	106	64.28	0.17	75	181
1985	69.09	0.12	159	64.33	0.17	124	283
1986	68.61	0.15	146	63.45	0.16	68	214
1987	69.35	0.13	92	64.76	0.25	69	161
1988	69.13	0.12	173	64.3	0.16	73	246
1989	69.01	0.09	215	64.31	0.14	102	317
1990	69.10	0.14	153	64.0	0.16	88	241
1991	69.43	0.09	187	64.84	0.19	102	289
1992	69.09	0.10	193	64.18	0.10	190	383
1993	69.43	0.09	264	64.10	0.11	164	428
1994	69.20	0.09	311	63.73	0.11	159	469
1995	69.50	0.07	399	63.98	0.14	138	537
1996	69.01	0.05	896	64.05	0.05	947	1843
1997	69.28	0.04	1147	64.16	0.05	1140	2287
1998	69.20	0.04	1180	64.03	0.04	1659	2839
1999	68.98	0.03	2448	63.73	0.04	1910	4358
2000	68.86	0.03	2141	63.80	0.03	2150	4291
2001	68.69	0.03	2431	63.48	0.03	2224	4655
2002	68.97	0.03	2239	63.86	0.03	2059	4298
2003	68.74	0.03	1882	63.72	0.05	1209	3091
2004	68.86	0.03	2503	63.71	0.03	2395	4898

Year(s)	Males			Females			Total number of birds
	Mean wing length (mm)	Standard error	Number of birds	Mean wing length (mm)	Standard error	Number of birds	
2005	68.86	0.03	2473	63.77	0.03	2551	5024
2006	68.68	0.03	2311	63.48	0.03	1976	4287
2007	69.10	0.02	3249	63.97	0.03	3176	6425
2008	68.85	0.04	1464	63.63	0.06	764	2228

Table 4. Data from adult Willow Warblers caught at individual breeding sites in the period April-June, with mean wing lengths (mm), standard errors and count of males and females. Data from individual birds are included once only in each year they are caught. Years are grouped where necessary to have sufficient data to enable use of FISAT to calculate male and female mean wing lengths and counts.

(a) Wicken Fen 1969-2008.

Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1969-71	66.90	0.17	126	61.35	0.19	48	174
1972-74	67.98	0.19	70	62.25	0.26	31	101
1975-78	67.71	0.20	80	62.85	0.26	40	120
1979-83	68.51	0.19	70	63.28	0.27	40	110
1984-85	68.99	0.16	73	64.02	0.21	34	107
1986-88	69.30	0.17	86	64.07	0.21	42	128
1989-91	68.67	0.18	76	63.63	0.17	42	118
1992-96	68.94	0.14	83	63.68	0.22	47	130
1997-99	69.02	0.14	77	64.06	0.18	54	131
2000-04	69.08	0.18	56	63.94	0.29	40	96
2005-208	68.57	0.21	70	63.86	0.21	31	101

(b) Chew and Gordano Valleys, 1976-2007

Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1976-80	68.21	0.17	107	62.33	0.34	12	119
1981-85	68.51	0.12	91	64.17	0.24	50	141
1986-89	68.85	0.17	71	64.68	0.27	50	121
1990-92	68.86	0.12	95	64.39	0.20	64	159
1993-94	68.69	0.11	142	63.26	0.16	55	197
1995	68.83	0.16	59	63.01	0.29	33	92
1996-97	68.23	0.15	73	63.11	0.19	91	164
1998-99	68.40	0.21	79	62.51	0.27	45	124
2000-03	68.25	0.19	60	64.11	0.30	72	132
2004-07	68.58	0.18	59	63.96	0.26	39	98

(c) Kippo Wood, 1988-2007

Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1988-92	68.25	0.20	90	62.66	0.27	24	114
1993-94	68.20	0.17	112	63.23	0.26	26	138
1995	68.96	0.13	95	64.13	0.19	109	204
1996	68.29	0.17	121	62.94	0.19	74	195
1997	68.84	0.13	121	63.72	0.21	124	245
1998-99	68.12	0.19	104	62.96	0.24	51	155
2000	68.76	0.14	116	63.01	0.16	51	167
2001	68.39	0.19	66	63.17	0.25	25	91
2002-04	68.79	0.13	104	63.7	0.27	45	149
2005-08	68.42	0.17	83	63.03	0.18	31	114

(d) Loch Eye, 1994-2007

Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1994-95	69.01	0.22	58	63.68	0.23	27	85
1996-97	69.09	0.15	82	63.66	0.17	39	121
1998-99	69.33	0.16	64	63.97	0.16	46	110
2000-01	69.63	0.18	55	64.24	0.23	40	95
2002-04	68.45	0.17	91	63.69	0.18	37	128
2005-07	68.70	0.20	65	63.15	0.23	31	96

Table 5. Data from Bardsey Island of adult Willow Warblers caught on spring migration, March-June, 1956-2007, with mean wing lengths (mm) for each period, standard errors and count of males and females. Data from individual birds are included once only in each year they are caught.

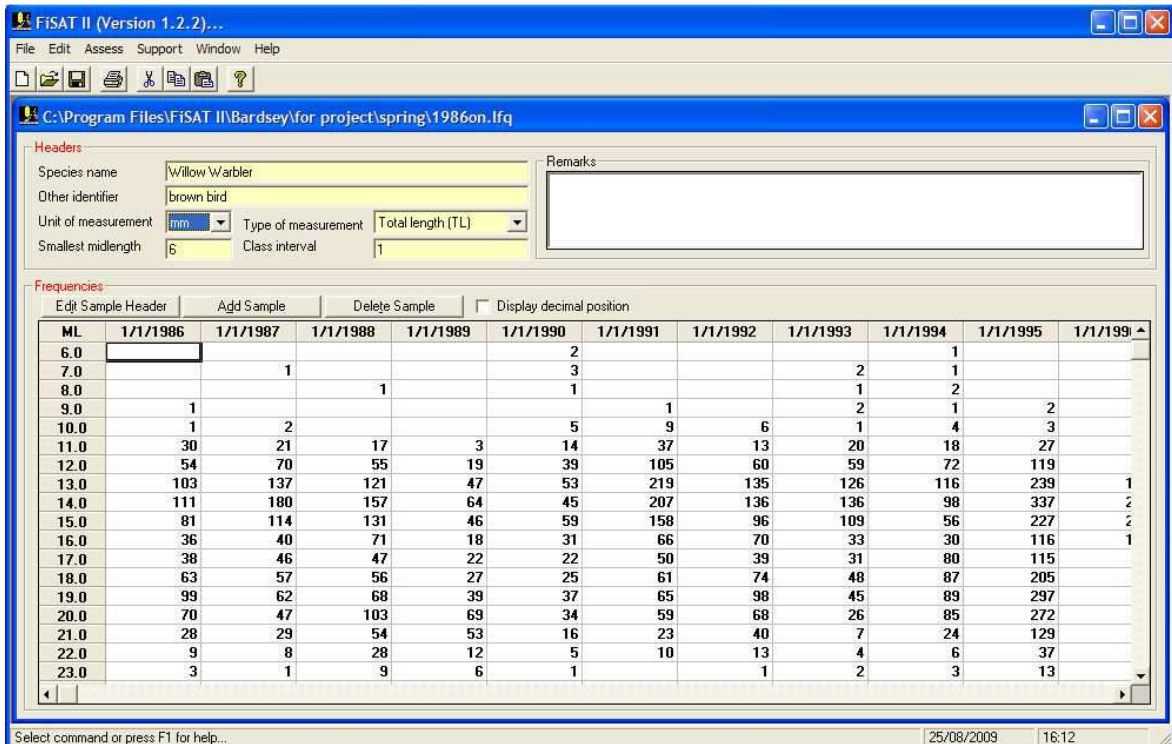
Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1956	67.61	0.11	218	62.53	0.10	121	339
1957	68.42	0.07	318	62.96	0.20	35	353
1964	67.05	0.13	114	62.30	0.13	119	233
1967	67.11	0.19	62	62.48	0.12	196	258
1968	67.42	0.25	29	61.92	0.19	66	95
1969	67.49	0.14	88	62.67	0.11	142	230
1970	67.04	0.15	58	62.36	0.12	155	213
1974	68.44	0.10	182	63.56	0.11	166	348
1975	68.35	0.17	82	63.86	0.09	219	301
1976	68.65	0.13	205	63.14	0.07	367	572
1977	68.78	0.20	63	63.34	0.13	103	166
1978	68.38	0.14	138	63.19	0.07	378	516
1979	68.58	0.17	73	63.80	0.29	53	126
1980	68.54	0.10	257	63.53	0.12	135	392
1981	69.08	0.13	126	63.80	0.11	190	316
1982	67.78	0.38	22	63.13	0.15	67	89
1983	68.75	0.12	126	63.84	0.12	146	272
1984	68.41	0.10	145	63.36	0.08	379	524
1985	68.99	0.09	268	63.88	0.05	657	925
1986	69.06	0.08	308	63.66	0.07	419	727
1987	68.85	0.10	253	63.73	0.06	562	815
1988	69.65	0.08	346	64.11	0.06	575	921
1989	69.77	0.10	223	64.03	0.09	202	425
1990	69.61	0.12	102	64.10	0.13	290	392
1991	68.88	0.09	262	63.69	0.05	808	1070
1992	69.09	0.08	330	63.89	0.06	519	849
1993	68.69	0.11	157	63.73	0.07	495	652
1994	68.63	0.08	389	63.32	0.08	384	773
1995	69.21	0.04	1072	63.91	0.04	1068	2140
1996	69.26	0.09	280	64.28	0.05	868	1148
1997	69.61	0.09	293	64.18	0.08	343	636
1998	69.36	0.13	103	64.10	0.16	103	206
1999	69.00	0.09	250	63.58	0.10	192	442
2000	68.50	0.12	158	63.47	0.10	192	350.2

Year	Males			Females			Total count
	Mean wing length (mm)	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
2001	68.12	0.13	183	63.07	0.08	264	447
2002	68.88	0.11	135	63.87	0.20	74	209
2003	68.62	0.13	127	63.57	0.15	69	196
2004	69.23	0.19	47	63.95	0.23	63	110
2005	68.65	0.09	215	63.59	0.11	170	385
2006	68.58	0.16	42	63.49	0.11	107	149
2007	68.88	0.12	87	64.33	0.15	106	193

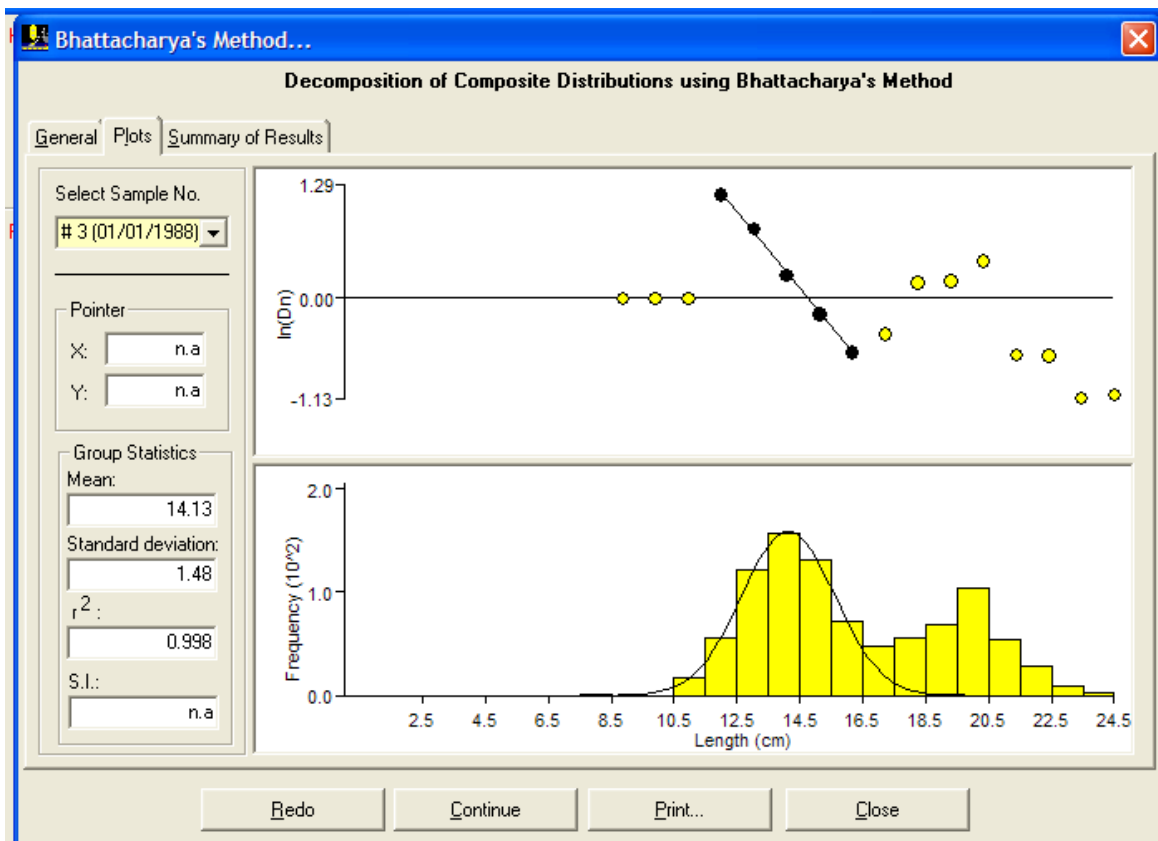
Table 6. Data from Sandwich Bay of adult Willow Warblers caught on spring migration, March-June, 1958-2007, with mean wing lengths (mm) for each period, standard errors and count of males and females. Data from individual birds are included once only in each year they are caught. Years are grouped where necessary to have sufficient data to enable use of FISAT to calculate male and female mean wing lengths and counts.

Year	Males			Females			Total count
	Wing	Standard error (mm)	Count	Mean wing length (mm)	Standard error (mm)	Count	
1958-62	67.20	0.24	24	62.16	0.25	74	98
1963-65	66.13	0.14	56	61.18	0.17	66	122
1970-72	66.46	0.26	62	60.88	0.25	21	83
1991-92	67.67	0.35	31	62.32	0.19	49	80
1993-94	67.59	0.17	91	62.13	0.19	54	145
1995-96	68.14	0.14	105	63.35	0.32	26	131
1997-98	67.40	0.17	52	62.92	0.21	61	113
1999-03	68.12	0.15	78	63.51	0.19	64	142
2004-08	69.01	0.16	33	63.95	0.26	67	100

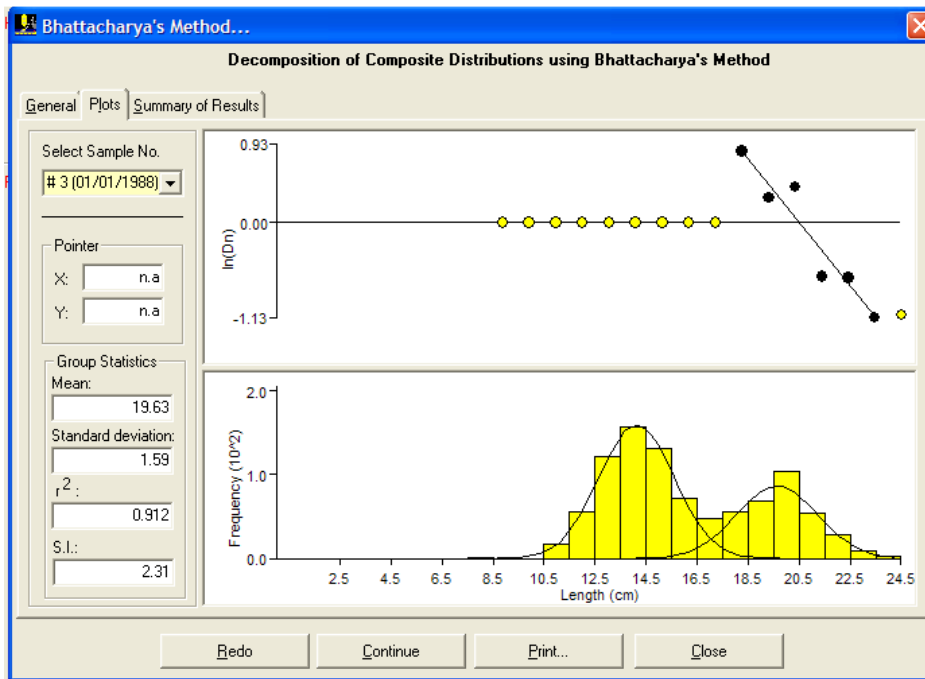
(a)



(b)



(c)



(d)

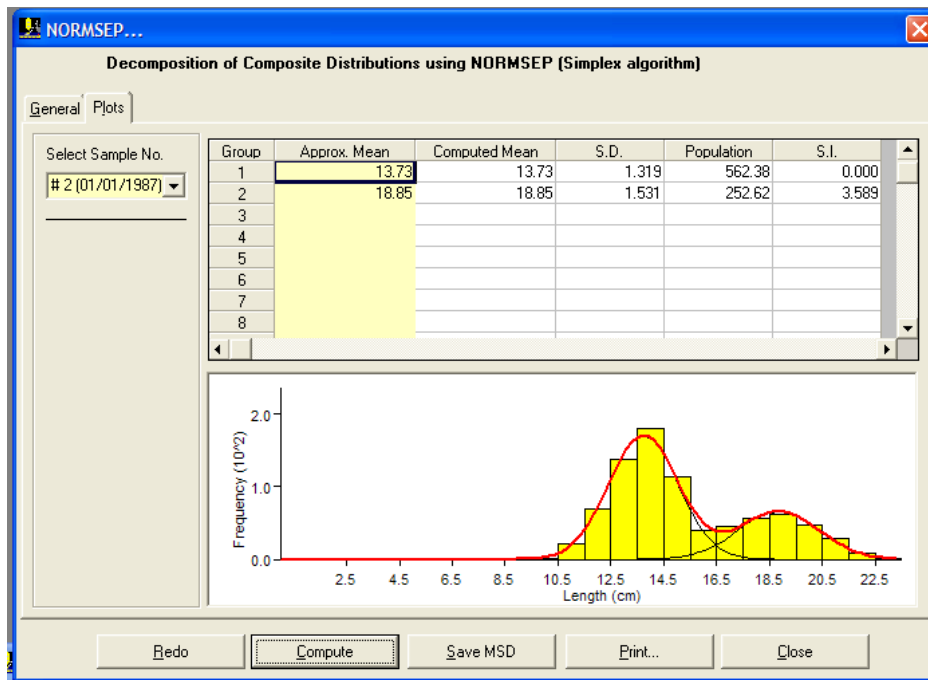


Figure 36. Procedure for analysis of data using FISAT_II software to obtain male and female mean wing lengths, counts and standard errors: (a) input counts of wing lengths by year; (b)&(c) estimate regression lines for data points (differences of natural logarithms of adjacent length frequencies) for each population distribution (d) compute to refine results using Normsep (www.fao.org, 2009).