J Ornithol (2007) 148 (Suppl 2):S495–S499
DOI 10.1007/s10336-007-0215-4

ORIGINAL ARTICLE

Climate change and spring migration in the Yellow Wagtail *Motacilla flava*: an Afrotropical perspective

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Received: 21 August 2006 / Revised: 8 August 2007 / Accepted: 8 August 2007 / Published online: 1 September 2007

Abstract Timing of pre-migratory fattening among Yellow Wagtails *Motacilla flava* wintering in Nigeria pre-1980 is compared with that in the period 2004–2006 to determine whether this has been affected by trends towards earlier spring phenology in Europe over the same period. Wagtails wintering in northern Nigeria showed later fattening, in central Nigeria similar timing, and in southern Nigeria earlier fattening, than comparable pre-1980 populations. Later fattening in the north may be related to environmental degradation and difficulties faced by such populations in advancing migration date because of the proximity of the moulting period. Consistency of timing in central Nigeria may be related to the regular arrival of drought-breaking rain at this latitude around the start of April, and earlier fattening in the southerly winterers may reflect a general lack of constraint for such populations, which gain weight in wet season conditions, several weeks after the end of moult. Since southern winterers breed furthest north, advancement of spring arrival time should therefore be more pronounced among populations breeding in northern Europe.

Keywords Migration · Moult · Climate change · Pre-migratory fattening · Wet/dry season cycle

Communicated by F. Bairlein.

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Introduction

The current upsurge of interest in the effects of changing climate on the movements of migratory birds has focused mainly on the significance of variation in the phenology of north temperate breeding areas (Møller et al. 2004), with relatively little attention paid to factors operating in the tropical zones where many migrants spend the northern winter. Interest has therefore centred mainly on the timing of arrival on breeding grounds in Europe and North America in response to long-term trends towards warmer springs, or to annual variation related to, for instance, the North Atlantic Oscillation (Hüppop and Hüppop 2003). This temperate zone perspective has been reinforced by the notion that migration timing is endogenously controlled in long-distance migrants (Both and Visser 2001), or else that the date of departure from the tropics is endogenous, with facultative responses to climate occurring only once temperate areas have been reached (Zalakevicius et al. 2006).

More recently, a number of studies have considered the effect of climate in tropical staging or wintering areas on the timing of migration, focusing mainly on the possible effects of annual variation in temperature and rainfall in the tropics on the spring arrival schedule of temperate breeding migrants (Gordo et al. 2005). Here, I will develop this theme by considering factors operating in the wintering areas of trans-Saharan migrants that might affect their ability to adjust migration in response to the changing climate of breeding areas in Europe. The nature of the constraints emerging from the varied wintering environments encountered by sub-Saharan migrants will be discussed in the context of a comparison of recent data on timing of pre-migratory fuel deposition with similar data collected over 30 years ago.

Methods

The Yellow Wagtail *Motacilla flava* is an insectivorous songbird that breeds across the Palaearctic and migrates to spend the northern winter almost exclusively in the Palaeotropics, including sub-Saharan Africa, where they perform a pronounced leapfrog migration (Bell 1996). The species was a focus for migration studies carried out in Nigeria in the 1960s and 1970s, and number of published datasets are therefore available for that period indicating the timing of fuel deposition ahead of pre-nuptial migration (summarised in Wood 1992). Over the period 2004–2006, I measured wagtail weights in three different sites in Nigeria, during studies timed to coincide with the periods of fattening in each locality, as indicated by these earlier datasets.

Mist-netting aimed at trapping Yellow Wagtails in their foraging habitat was carried out at Jos (9°49′N, 8°54′E) in April 2004, Nguru (12°52′N, 10°27′E) in March 2005, and Obudu Plateau (6°22′N, 9°23′E) in April 2006. The site at Jos comprised an area of commercially farmed tomato and pepper fields, irrigated by water pumped from flooded tin workings. At Nguru, mist-netting was carried out in flood recession farmland cultivated by subsistence farmers growing primarily cowpea, okra and groundnuts. At Obudu plateau, the study was carried out in improved pasture in the vicinity of a commercial dairy farm. A similar protocol was followed at each site, involving the siting of two 12-m mist nets in the vicinity of concentrations of foraging wagtails, with continuous re-positioning of nets to counter habituation and avoidance of the nets. Trapped birds were sexed and aged, and weighed to the nearest 0.1 g. At Nguru and Obudu Plateau, some additional birds were trapped using a whoosh net.

Results

Weights of wagtails in populations sampled in 2004–2006 are presented for comparison with pre-1980 datasets obtained at similar latitudes in Nigeria in Fig. 1. Data obtained at Nguru in 2005 are compared with a dataset recorded at Kano (12°0′N, 8°31′E) in 1974–1975 (Fig. 1a). Data from Jos in 2004 are compared with samples obtained in the same area in 1964 and in 1974–1975 (Fig. 1b), and data from Obudu Plateau in 2006 are compared with a dataset obtained at Ibadan (7°23′N, 3°54′E) in 1963 (Fig. 1c). In each case, the recent data are transformed and summarised for convenient comparison with the historical datasets. In the case of Jos (historical) and Kano, weights were obtained from roosting birds at sunset (Smith and Ebbutt 1965; Wood 1992), so Jos (recent) and Nguru data obtained at various times through the day were corrected to sunset, assuming a linear weight increase of 1.2 g during hours of daylight. Weights obtained at Obudu Plateau were corrected the same way, but this time to dawn, when the data for the Ibadan sample were obtained (Ward 1964). Comparability with the latter was then achieved by transformation of corrected weights to estimates of lipid content, using a relationship derived empirically for the species (Fry et al. 1970).

Comparison of weight data for male wagtails at Nguru with that obtained at Kano over the same calendar period indicates that Nguru birds were fattening significantly later [SS (intercept) = 92.85, $F_{1,83} = 17.723$, $P < 0.0001$, SS (combined slope) = 226.6, $F_{1,83} = 43.253$, $P < 0.0001$], and that among females at Nguru there was no evidence of any significant fattening over the same period (Fig. 1a). By contrast, at Jos the data obtained in 2004 indicated fattening occurring on an essentially identical schedule to that seen in the same area in 1963 (Fig. 1b). The comparison of Obudu Plateau and Ibadan indicates some evidence for earlier fattening at this southern latitude in 2006 than in 1964 (Fig. 1c). Caution is required, however, since most of the heavy birds seen in early April at Obudu Plateau were males, while the sex of individual birds in the Ibadan sample was not recorded, though overall ratio for April was recorded at M:F = 1:1.8. The sex ratio in the Obudu Plateau sample was approximately 1:1, so statistical comparison requires appropriate weighting. Anova of $\log_e$ lipid fraction for the first half of April, with a weighting of 0.55:1:1 for Obudu males:Obudu females:Ibadan, indicates significantly greater lipid levels in the Obudu Plateau sample over this period (SS = 3.401, $F_{1,40} = 13.893$, $P = 0.0006$). Back transformation of the least squares estimates indicates a median lipid fraction of 7.1% for Ibadan, and a (weighted) median of 13.6% at Obudu Plateau.

Discussion

The overall picture emerging from the comparison of recent data on pre-migratory fattening with the pattern prevailing 30 or more years ago, is one of contraction towards the median. Fattening was found to be later in the north, where wagtail populations fatten relatively early, no change was detected in central latitudes, and earlier fattening was found in the south where it occurs relatively late. The general trend towards later fattening among more southerly populations is related to the leapfrog migration pattern prevailing in the species. Populations "over-wintering" further south have more northerly breeding areas, the later phenology of which necessitate a later migration schedule. This spatio-temporal arrangement of different breeding populations means that they encounter very

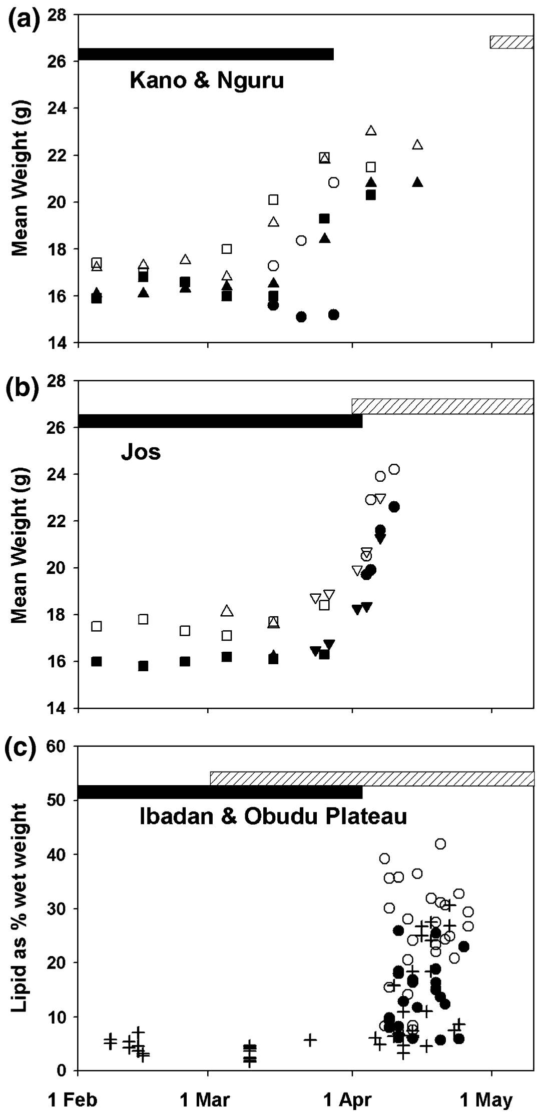

Fig. 1 Pre-migratory fattening by Yellow Wagtails *Motacilla flava* in Nigeria pre-1980, compared with 2004–2006. **a**,**b** Mean weights for continuous periods that vary from 1 to 11 days depending on rate of change, and also the number and temporal distribution of available data. **c** Actual lipid fraction for individuals in a sample from Ibadan in 1963, and estimates of lipid fraction based on weight for Obudu Plateau. *Solid bar* moulting period, *stripped bar* rainy season, *open inverted triangle* and *filled inverted triangle* Jos 1964 (*open symbols* males, *filled symbols* females), *open square* and *filled square* Jos, Kano 1974; *open triangle* and *filled traingle* Jos, Kano 1975; *open circle* and *filled circle* Jos 2004, Nguru 2005, Obudu Plateau 2006; *plus symbols* Ibadan 1963. Moult may be completed slightly earlier among the northernmost wintering populations, cf. Bell (2006), Wood (1978)

different environments during the period immediately prior to migration back to the breeding grounds, and this may profoundly effect the extent to which they experience directional selection for migration timing as a result of climate change in the breeding area.

The timing of the wet/dry season cycle is of overwhelming significance in this context. The dry season is relatively short in the south, lasting only about 4 months from November to March at the latitude of Ibadan and Obudu Plateau (Fig. 1c). At Jos, the dry season lasts approximately 6 months, usually ending abruptly with heavy downpours around the beginning of April (Fig. 1b), while at the latitude of Kano/Nguru, the dry season lasts 8 months, with drought-breaking rain arriving only in May (Fig. 1a). Consequently, wagtail populations that remain in the north of Nigeria are faced with the need to acquire fuel for the trans-Saharan migration back to Europe in an environment where no rain has fallen for more than 7 months, during which period there is a steady decline in the availability of insect food (Wood 1979).

Under these circumstances, it might be expected that wagtails would respond well to selection for earlier migration, since this would mean fattening earlier in the year when insect availability has declined less far. However, one further consequence of the early migration schedule of these northern wintering populations is a wide overlap between pre-migratory fattening and the partial pre-alternate moult that takes place during February and March (Fig. 1a), when wagtails replace all feathers except remiges. The competing energetic demands of moult may mean that it is especially difficult for these populations to adjust their migration timing to an earlier schedule, despite the benefit of greater food availability.

Wagtails over-wintering at this latitude in west Africa rely heavily on habitats associated with permanent water sources, including the *Fadama* (floodplain) cultivation foraged over by wagtails at Nguru, which relies on a high water table persisting throughout the dry season. Such farmland relies on the seasonal ebb and flow of floodwaters that are replenished during the rainy season. However, at Nguru in recent years the floods have been so severe that standing water has persisted over large areas right through the dry season, rendering up to 80% of farmland unusable (Anonymous 2005). Such a catastrophic decline in the availability of wintering habitat over a short period may be behind the late fattening schedule seen at Nguru in 2005, from where a raft of evidence emerged for overcrowding, consistent with a large local wintering population being squeezed into a small area of remaining habitat (Bell 2006). Overwinter survival may be practicable at such high densities (though mean female weight is well below the normal mid-winter minimum; Fig. 1a), but acquiring sufficient surplus to lay down fuel reserves appeared to be problematic.

This illustrates what may be a more general problem facing migrants wintering in the arid regions on the southern edge of the Sahara, which is heavy dependence on specialised habitats providing the minimum requirements for survival. Initial cost in fitness terms of the loss of such habitats may therefore be depressed breeding output caused by late arrival on the breeding grounds. If delayed preparation for migration is attributable to habitat loss, the effects are likely to be localised, with a “normal” schedule prevailing elsewhere in the Sahelian region where no catastrophic flooding has occurred. Such effects are much less likely for populations wintering further south, which benefit from being able to prepare for migration under rainy season conditions. At the latitude of Jos, preparation for migration coincides with the onset of rains (Fig. 1b), which means that local populations benefit from a sudden increase in food availability just at the time it is required (Bell 2007). Emergence of termite swarms and other insects occurs across a wide range of habitats, enabling insectivorous birds to escape from specific habitats occupied during the dry season.

The coincidence of drought-breaking rain with pre-migratory fattening by populations within this latitudinal range is significant in the context of advancing spring phenology in their European breeding areas. A population long accustomed to food abundance in the period of pre-migratory fattening may evolve a strategic reliance on the annual spike of food availability associated with the first rains of the year. It may therefore be difficult for such populations to advance the timing of migration in response to conditions in the breeding area, as they effectively have to wait for the rains to arrive. It may also be significant that moult is just ending at the time the rains arrive and pre-migratory fattening begins (Fig. 1b), which means that earlier pre-migratory fattening will lead to overlap with moult. These constraints may have contributed to the close correspondence between the progress of fattening at Jos in 2004 and that seen 40 years earlier in the same area (Fig. 1b).

If, on the other hand, selection for earlier migration becomes so strong that local populations do begin to migrate earlier in the year, the result could be a shift of wintering latitude. They may either shift their non-breeding range further south to the latitude reached by rains at this earlier date, or alternatively abandon altogether the strategy of relying on the rains to assist pre-migratory fattening, and, having lost the incentive to extend migration, shift their wintering range further north to the Sahelian region. The situation is much simpler for populations wintering further south still, where fattening begins several weeks after the beginning of the rains (Fig. 1c). The late migratory schedule of these populations also means that there is much less danger of significant overlap with the end of moult. A shift to an earlier migration schedule therefore makes very little difference to conditions for fattening, and this may be reflected in the apparently earlier fattening schedule seen at Obudu Plateau in 2006, compared to Ibadan in 1963.

Given the degree of variation, both environmental and intrinsic, in the constraints experienced by migrants wintering in different areas of sub-Saharan Africa, there is every reason to expect corresponding variation in the evolutionary response to advancing spring phenology in Europe. The comparison of the current timing of pre-migratory fattening with that over 30 years ago is puzzling when viewed solely against a background of generally advancing phenology on the breeding grounds, but becomes much more readily comprehensible when viewed in the context of varying sets of constraints encountered by different populations. The fact that migration follows hard on the later stages of moult among northern wintering populations may outweigh any selective advantage gained by earlier arrival on the breeding grounds, preventing a shift to an earlier endogenous timing of migration and rendering environmentally induced delay more likely. Although later migrating populations wintering in central latitudes are less constrained by moult, they may be similarly constrained from evolving an earlier migration schedule by the great advantage to be gained by waiting to fatten in drought-breaking rains that occur, on average, in early April. If rains happen to arrive late, however, this may cause significant delay in preparation and departure on migration. The fewest constraints apply to the most southerly wintering and latest departing populations, which migrate several weeks after the end of moult and the beginning of local rains. These populations may therefore be the most likely to respond to selection for earlier migration, in which case an advance of arrival time in the breeding area should be most easily detectable for this species in the northern areas of Europe where these southerly wintering populations breed.

The amount of data that is available to provide a picture of the way that migratory birds respond to variation in conditions in the vital weeks before pre-nuptial migration remains relatively small. This gap in knowledge is likely to create great difficulty for the development of useful models of the responses of long-distance migrants to climate change, so it is vital that resources be invested to obtain such data, particularly in the west African wintering areas that host the majority of European trans-Saharan migrants. Urgent attention should be paid to investigations of how birds resolve the conflicting requirements of moult and pre-migratory fattening, the physiological and demographic effects of shifting habitats in unpredictable Sahelian wintering areas, and the consequences of annual variation in timing of rains for populations wintering in central latitudes. Needless to say, there is also a need for regular gathering of information on numbers and period of residence of overwintering migrants, to assess medium and long-term trends in relation to the much more comprehensive picture derived from the good quality data available for breeding and staging areas across much of Europe.

Acknowledgments Thanks to John Atsen and Chris Otata-Odey of the AP Leventis Institute for field support at Jos and Nguru respectively, and also to Phil Hall and Ulf Ottosson. Thanks also to Andy Dunn, John Oates, Columbus Ikpe and Dennis Ogar for support during work at Obudu Plateau. Vic Smith and an anonymous reviewer provided valuable comments on a draft of the manuscript.

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