Social interactions, moult and pre-migratory fattening among Yellow Wagtails *Motacilla flava* in the Nigerian Sahel

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Summary

Yellow Wagtails were studied at Nguru, northern Nigeria, just before pre-nuptial migration, and the findings are compared with results of similar studies carried out elsewhere in the country. Wagtails foraged mainly on farmland, as recently observed elsewhere in Nigeria, but in contrast to 30 years earlier when they fed mostly around cattle and at water margins. Males defended compact territories in which females appeared to feed opportunistically, contributing to a high level of aggression and indicating a densely packed population. Subspecies, age and sex composition were consistent with previous studies in northern Nigeria. When compared with more southerly wintering populations, the preponderance of males and adults, and a diverse range of subspecies characteristic of breeding areas in southern Europe, indicate marked differential and leap-frog migration patterns. Pre-migratory fattening was detected only in adult males, in contrast to previous studies in the same area showing fattening across all population classes over the same calendar period. Together with low weights among non-fattening birds, lack of overlap between fattening and moult, and a high density and level of agonistic behaviour, this suggests a population under stress, consistent with recent catastrophic loss of available habitat in the local area.

Résumé

Intéractions sociales, mue et engraissement pré-migratoires chez la Bergeronnette printanière *Motacilla flava* au Sahel nigérian. Les Bergeronnettes printanières ont été étudiées à Nguru, nord du Nigéria, juste avant la migration prénuptiale, et les résultats sont comparés à ceux d'études similaires menées ailleurs dans le pays. Les bergeronnettes se nourrissaient surtout dans les champs, comme on l'a récemment observé ailleurs au Nigéria, mais non plus comme 30 ans plus tôt surtout près du bétail et au bord de l'eau. Les mâles défendaient de petits territoires où les femelles semblaient se nourrir de façon opportuniste, ce qui contribuait à un haut niveau d'agressivité et indiquait une forte densité de population. La répartition en sous-espèces, âges et sexes correspondait à celle des études précédentes dans le nord nigérian. La comparaison de cette population à celles hivernant plus au sud, la prépondérance des mâles et des adultes ainsi qu'une distribution des sous-espèces caractéristiques des zones de reproduction au sud de l'Europe, indiquaient un système de migration différentiel prononcé et en saute-mouton. L'engraissement pré-migratoire n'a été mis en évidence que chez les mâles adultes, contrairement à des études antérieures dans la même région qui montraient l'engraissement pour toutes les classes de population durant la même période. Aussi bien les poids faibles parmi les sujets n'ayant pas engraissé que l'absence de chevauchement entre engraissement et mue de même qu'une forte densité et le niveau élevé d'agressivité, révèlent une population sous tension, ce que confirme la récente et catastrophique perte d'habitat disponible dans la région locale.

Introduction

For migratory birds, and particularly long-distance migrants, the period immediately prior to pre-nuptial migration is critical. Preparation and departure must be timed to enable arrival on the breeding grounds at the optimal time to maximise breeding success (Møller 1994). Insectivorous Palaearctic migrants wintering just south of the Sahara need to build up a large fat depot to enable crossing of the desert, at a time when many wintering areas have experienced no rain for up to half a year, and arthropod availability is at an annual low. Many such migrants also undergo substantial moults in late winter, creating an additional energetic requirement that may conflict with the need to acquire an energy surplus to lay down fat reserves.

The Yellow Wagtail *Motacilla flava* is an insectivorous Palaearctic migrant that has been relatively well studied in its sub-Saharan wintering area, mainly due to the relative ease of trapping large numbers at mass roosts (Smith & Ebbutt 1966, Fry *et al.* 1972, Wood 1978). The species has marked leap-frog and differential migration patterns, the latter partly mediated by a gradual southerly shift in population over the course of the winter that varies in degree among population age and sex classes. It has also been shown to depart the wintering ground in sequence according to breeding latitude, with more southerly breeding (and northerly wintering) populations migrating earlier (Wood 1975, 1992).

In order to understand how the species manages its energy in the period prior to migration, I studied pre-migratory fattening, moult, and social organisation in a population of Yellow Wagtails in the Sahel of N Nigeria, where energy trade-offs may be particularly acute. I compare results with previous studies carried out in the same area and elsewhere in Nigeria, in the context of short- and long-term changes in the environment, and ideas about the origin of migration patterns.

Methods

Fieldwork was carried out between 12 and 31 Mar 2005 at Nguru (12º52´N, 10º27´E) in N Nigeria. Nguru is situated at the N edge of the floodplain of the Hadejia and Jama'are rivers, where the annual flood supports a dry season "recession farming" economy, in which plots are cultivated by hand in the wake of receding flood waters (Hollis *et al.* 1993). Primary crops are cowpea, groundnuts, okra and onions, and such farmland forms the principal foraging habitat of wagtails wintering in the area. The study area comprised a *c.* 50 ha strip of farmed land, sandwiched between dry, uncultivated savanna to the north and flooded areas to the south supporting extensive stands of *Typha australis*.

Mist netting was carried out daily using two 12-m, four-panel nets in cultivated plots either side of the main Nguru–Hadejia highway, between 3 and 5 km west of Nguru. Mist-netting rapidly became confined to the 2–3 h following sunrise, and 1–2 h before sunset, owing to a persistent NE wind that prevailed in the middle of the day. Individual netting sessions were rotated around six sites scattered across the cultivated area, to minimize habituation to, and avoidance of, the nets by foraging wagtails. Each captured wagtail was ringed, weighed using a spring balance, and aged and sexed where possible using standard criteria (Alström & Mild 2003). Diagnostic subspecific characters were recorded, and each bird was also examined for moult.

Mist-netting operations afforded ample opportunity to observe social interactions and territoriality among the focal populations. The variable plumage of the wagtails in the area meant that individuals became quickly recognisable, enabling mapping of some of the territories near the nets. This proved possible at the five out of six sites where netting was carried out on at least five days.

Weights were obtained at varying times of day, so for analyses Nguru weights are corrected to sunset (18h30) assuming a linear weight gain of 1.2g during the hours of daylight (this applies to the analyses presented in Figs 1 and 2 and Tables 2 and 3).

Results

Subspecies, sex, and age

The 81 wagtails captured and examined varied greatly in subspecific characteristics, as determined primarily by colour and head markings Table 1). Most males were assignable either to *M. f. flava* or *M. f. cinereocapilla* (Fig. 1), while a few resembled the plumage variants *M. f.* "*dombrowskii*", with a relatively dark blue crown and blue-black ear coverts, or *M. f.* "*superciliaris*", with an entirely blue-black crown, both with a white supercilium (Fig. 2; Alström & Mild 2003). The majority of females resembled typical *M. f. flava*, but some resembled females of the dark-headed populations of the Mediterranean basin, either lacking a pale supercilium or with a relatively dark crown (Alström & Mild 2003), and in many cases showing both of these characteristics. Females were assigned to subspecies as follows: pale head and well-defined supercilium = *M. f. flava*; dark head and ill-defined supercilium = *cinereocapilla*; any other = "intermediate" (considered equivalent to "*dombrowskii*" or "*superciliaris*" among males). Two birds had entirely green crowns and bright yellow supercilia and underparts (Fig. 3), and were assigned as females as both had shorter wings than any of the males examined.

The sex ratio in the mist-net sample showed a slight preponderance of males, and of the birds that it was possible to age accurately, only one in five proved to be a first winter bird (Table 1).

Table 1. Trapped wagtail age, sex and "subspecies" categories.

	green-headed	*flava*	"*dombrowskii*"	"*superciliaris*"	*cinereocapilla*	Total
Adult ♂		13	2	3	10	28
1st-winter ♂		3		2	3	8
Unknown ♂		4	2		2	8
			intermediate			
Adult ♀	2	15	4		3	24
1st-winter ♀			3		2	5
Unknown ♀		5	1		2	8
Total	2	40	17		22	81

Weight

Four birds were retrapped on a later date (Fig. 4), and the two that were still moulting when retrapped, both of which were territory-holding males, had lost weight. One of these birds was also retrapped twice on the date of first capture, showing a marked

Figure 1. Male *M. f. flava* (left) and *M. f. cinereocapilla.*

Figure 2. Male *M. f.* "*dombrowskii*" (left) and *M. f.* "*superciliaris*".

decrease in weight over the course of a few hours (Fig. 4). Since short-term weight loss may have been an effect of the capture itself, retraps are excluded from subsequent analyses of weight. No weight increase over time was detectable among

Figure 3. Female with green crown and yellow supercilium.

females (mean weight 15.3 g) or first-winter males (mean 16.7 g), but adult males increased steadily in weight at a mean rate of 0.25g per day (Fig. 4, Table 2). This compares with a rate of 0.43g per day in a population sampled using a similar protocol on farmland near Jos in central Nigeria (9º49´N, 8º54´E) in early April 2004 (Bell in press), corresponding to a prediction that southerly wintering populations should fatten more quickly (see Discussion). The difference between the two studies approaches significance (ss = 8.867, $F_{1,120}$ = 2.195, *P* = 0.07 one-tailed, 95% confidence interval for the difference of –0.058 to 0.406), despite the high error variance for slope inherent in data sets of this kind (Bell in press).

The trends in weight at Nguru contrast sharply with those indicated by a study carried out within 1° of latitude of Nguru at Kano (12º0´N, 8º30´E), where a marked increase in weight was noted among both males and females over the same calendar period in two successive years (Wood 1976, 1992). Trends differ significantly between the two datasets for both males and females (Table 3). Nguru adult males, though increasing in weight, did so around 6–8 days later than males in the earlier sample (Fig. 4). Nguru females were also significantly lighter than females sampled at Kano prior to the start of pre-migratory fattening in early March (Fig. 5).

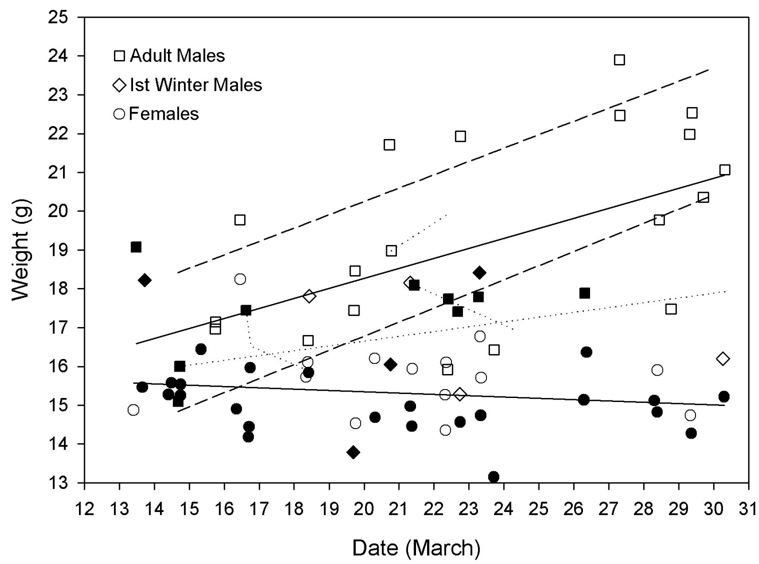

Figure 4. Weights of Yellow Wagtails at Nguru, 2005. Solid symbols indicate moulting birds. Solid regression lines: adult males (upper) and females (lower). Dashed lines: regressions for males and females in a 1974 sample from Kano (Wood 1976). Dotted lines: weight changes in retrapped birds.

Table 2. Analysis of covariance of weights of Yellow Wagtails at Nguru, March 2005. Model simplification proceeds with removal of non-significant levels of the interaction between sex-age category and date, followed by removal of the age factor within females only, to give the minimum adequate model.

	df	*ss*	*ms*	*F*	*P*
Residual	57	131.83	2.313		
Date x Adult ♀	1	1.755		0.759	0.387
Date x Adult ♂	1	50.09		21.66	<0.0001
Date x first-winter ♀	1	0.3984		0.172	0.680
Date x first-winter ♂	1	0.8487		0.367	0.547
Residual	60	134.83	2.247		
Adult ♀ x first-winter ♀	1	2.427		1.080	0.303
Residual	61	137.26	2.250		
♀ x first-winter ♂	1	12.72		5.653	0.021

Table 3. Analysis of covariance comparing weights of Yellow Wagtails at Nguru with those at Kano, March 1974.

		df	ss	ms	F	*P*
♂♂	Residual	82	430.77	5.253		
	Date x Site	1	4.050		0.771	0.383
	Residual	83	434.82	5.239		
	Site	1	92.85		17.723	<0.0001
	Date	1	226.6		43.253	<0.0001
♀♀	Residual	63	145.16	2.304		
	Date x Site	1	72.77		31.584	<0.0001

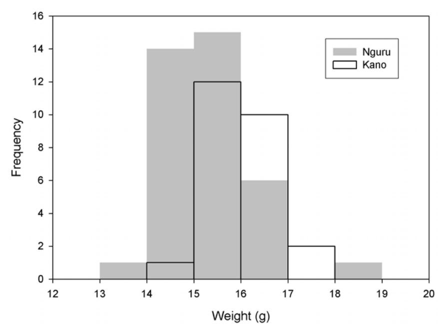

Figure 5. Weights of female Yellow Wagtails at Nguru in March 2005, compared to Kano, early March 1974 (data from Wood 1992). Mean weight for Kano birds is significantly greater (ss = 3.68, $F_{1,60}$ = 4.86, *P* = 0.03).

Moult

Moulting birds were found throughout the study, though the proportion showing evidence of moult declined (Fig. 6 and Table 4). Females may have lagged behind males in the progress of moult, as previously noted in Nigeria (Wood 1976). Most females were still moulting at the end of the study, but no moulting males were seen after 26 March (Fig. 6). Moult was complete in all of the heavy males seen during the latter part of the study period (Fig. 4), suggesting that pre-migratory fattening began in earnest only when moult had ended.

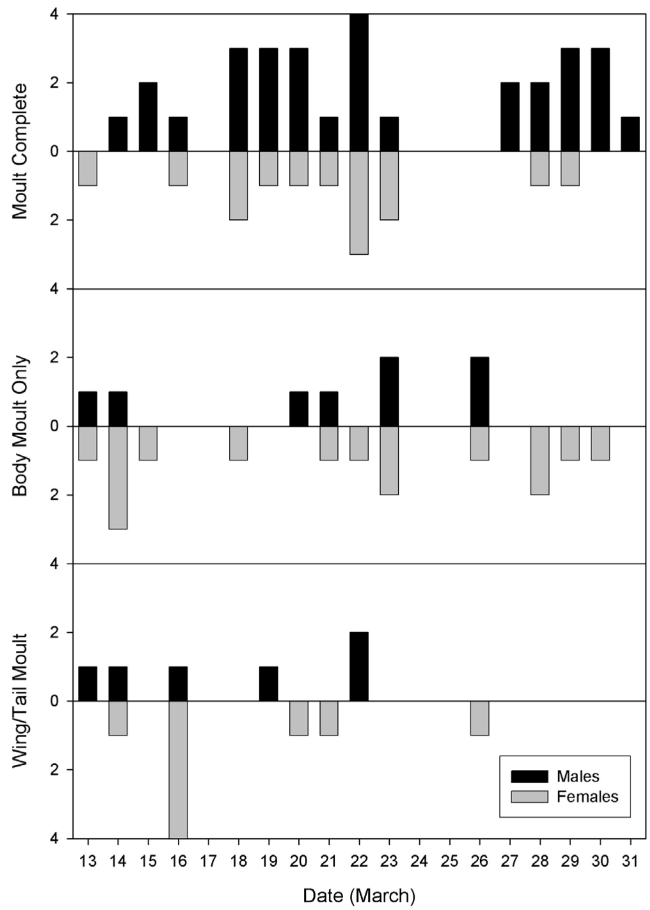

Figure 6. Numbers of wagtails in three consecutive stages of moult.

Table 4. Analysis of covariance of moult stage among Yellow Wagtails at Nguru, where birds showing wing and/or tail moult = 0, body moult only = 1, completed moult = 2. A binomial error structure and logit link function were used with scaled deviance to adjust for overdispersion of the data.

	df	scaled deviance	ms	F	*P*
Residual	78	96.46	1.279		
Date	1	6.10		4.77	0.032
Sex	1	4.32		3.38	0.070

Social Organisation

The area around at least five of the six mist-netting locations was divided up into territories, held almost exclusively by males and defended vigorously against intruding wagtails. Defended areas were small, typically no more than around 30 m in diameter. Some females also occupied consistent foraging areas, and some agonistic interactions between females were seen. However, only two females were seen to defend territories against intruding males. Most females appeared non-territorial, fed opportunistically in male territories, but retreated on the approach of the territory owner. Of the trapped birds, 11 were identified as territory holders, all of which were males. Nine of these were aged, and all except one were second-winter or older.

Two male wagtails appeared to abandon territories after being trapped, and on both occasions the vacant territory was immediately occupied and defended by another wagtail, in one case a female. The replacement male was subsequently trapped and was found to be older than one year, perhaps suggesting the presence of mature males among the non-territorial population.

Discussion

Social behaviour in relation to the environment

The territorial behaviour seen at Nguru is in sharp contrast to the situation on similar habitat at Jos in April 2004, where wagtails formed roving flocks of up to 200 birds (Bell in press) and showed no evidence of territorial behaviour. This difference almost certainly relates to differences in the agricultural regime. At Jos, fields of tomatoes and peppers relied on periodic irrigation with water pumped from nearby borrow pits. This was done in rotation, with different embanked enclosures irrigated in turn over a period of days, and wagtail flocks would generally alight in areas that had been recently irrigated. Flocking behaviour may therefore reflect the fact that food availability is always highest in the area most recently irrigated. By contrast at Nguru, the crops rely on a more stable high water table, and defence of territories is appropriate for dominant males at least.

Territories at Nguru were considerably smaller than areas used by breeding wagtails in Europe: generally several hectares when young are in the nest (Bell 1995).

The tightly packed territories of *c.* 0.1 ha also indicate a much higher density of wagtails than at Jos, where about 75 ha of farmland held around 300 wagtails (Bell 2006). A similar area at Nguru might hold up to 750 territories, and if the trap sample reflects overall sex ratio in the population, the density including non-territorial birds might be double this, especially if, as seems likely, there were many first-year and some adult males in the floating population. Competition to re-establish temporarily undefended territories might have contributed to the weight loss of two retrapped territory holders, since both frequented an area with particularly high densities and high frequency of agonistic interactions.

The concentration of wagtails in areas of cultivation at both Nguru and Jos contrasts with the situation observed in both areas in the 1970s, when the primary habit of wagtails on the Jos plateau was foraging around herds of cattle, while further north they were confined to water margins (Wood 1976). Very little evidence for association with cattle was seen in 2004–5, though cattle herds were searched for wagtails during initial prospecting at both at Jos and Nguru, and itinerant cattle herds regularly passed by study areas at both sites. At Jos, flocks of wagtails were occasionally seen to break off from foraging among crops to feed around a passing herd of cattle, but this was never seen to happen at Nguru.

This apparently widespread switch in behaviour may be related to the marked increase in the area under cultivation in Nigeria over the same period (Wint & Bourn 1994), particularly dry season cultivation (contrasting with a recent local decrease in this habitat at Hadejia-Nguru: Anon 2005, see below). The likely continuation of this trend might be beneficial for Yellow Wagtails, since dry season farming appears to create extremely valuable wintering habitat for the species. Interestingly, the change in wintering habitat parallels a switch in breeding habitat in Europe from pasture to arable land (Wilson & Vickery 2005).

Migration Patterns

The variable head colour of wagtails at Nguru gives clues to the breeding range of the population. Ringing recoveries indicate that wagtails wintering in Nigeria breed along a corridor from the central Mediterranean to the Baltic, and this corresponds to the variety of subspecies found in Nigeria in winter, mainly *M. f. flava*, but also *M. f. thunbergi*, *cinereocapilla* and *feldegg* (Wood 1982), the latter two occurring only in the north of the country, and *thunbergi* only in the south outside migration periods.

In this study only *M. f. cinereocapilla and M. f. flava* were identified with certainty. The former clearly breed in Italy or nearby, while the latter could potentially originate in a wide area from Hungary and Romania north to S Finland and NW Russia. However, given the general leap-frog pattern indicated by subspecies distribution and ringing recoveries, the southern portion of this zone is perhaps most likely.

No birds belonging to *M. f. feldegg* were found, but several corresponded to either "*dombrowskii*" or "*superciliaris*", two types conventionally considered intermediate between *M. f. flava* and *feldegg*, whose breeding origin is generally assigned to a zone of overlap between these two subspecies. Alström and Mild (2003) define this zone as extending from the Dalmatian coast of the Adriatic and its immediate hinterland, through N Albania and Macedonia to Bulgaria, and around the N coast of the Black Sea to the N Caucasus. The most likely breeding area for these birds, therefore, is the westernmost portion of this zone, stretching from Slovenia to Macedonia and W Bulgaria, where it overlaps with the zone of recovery for Nigerian-ringed birds.

The two green-headed individuals corresponded rather closely to *M. f. flavissima* or *M. f. lutea*, which breed in the British Isles and the lower Volga region, respectively. However both of these regions are well outside the zone of origin defined by ringing recoveries, and since green-headed birds are known from central European breeding populations (Alström & Mild 2003) it seems likely that these birds originated there.

The sex and age composition of the Nguru sample compared to wintering populations observed elsewhere in Nigeria is consistent with differential migration. The slightly male-biased sex ratio in the Nguru sample (54% male) is similar to that in the Kano study, where 62% (n = 207) and 60% (n = 236) males were obtained over the period Feb–Apr 1974–5 (Wood 1976). This contrasts with the sample obtained at Jos in April 2004 in which only 35% (n = 95) were male, which is consistent with an earlier study in the Jos area that showed the proportion of males declining from about 50% in mid winter to around 40% in mid-March (Wood 1976). The same study showed no temporal trend in the proportion of first year birds, which comprised 36% of the sample (n = 996), compared with 20% at Nguru. These data all tend to indicate a differential migration pattern in which adult males predominate in the populations wintering closest to the breeding grounds, with greater proportions of first-years and females in more distant wintering areas, as well as a greater tendency for females to move south over the course of the winter.

Comparison of the rate of increase in mean weight between Nguru and Jos is relevant to the hypothesis that differential and leap-frog patterns reflect variation in optimal latitude for fattening in relation to the timing of spring migration (Bell 1996, 2005, in press). Increase in mean weight in the Jos population was higher than among adult males at Nguru, corresponding to a prediction that southerly wintering populations fattening in the wake of drought-breaking rains should do so more quickly than those wintering in the north, which migrate before the end of the dry season. Any inference about the utility of the theory is weak, however, since conditions at Nguru in 2005 were far from typical, as discussed below. Moreover, the competing energetic demands of moult may have helped to reduce the rate at which the sampled cohort gained weight compared to the Jos birds, which fatten later in the year when moult is complete.

Timing of pre-migratory fattening

The lack of weight gain among females and the relatively late timing of weight gain among males, compared to a population sampled at Kano some 30 years earlier, confounds expectations arising from the tendency towards earlier spring migration among migrants breeding in Europe over the same period (Lehikonen *et al.* 2003). The Kano study indicates that male wagtails reached departure weight around the end of March, and females about a week later, which corresponds well with the usual arrival time and timing of the breeding season in the southern European breeding sites of locally wintering populations (Spina *et al.* 1994). In the population studied at Nguru, only the heaviest males would have been able to migrate at the end of March, and if the trend among adult males continued most would not be able to depart until well into April, while departure by females would be impossible until late in the month. Such late arrival on the breeding grounds would be likely to profoundly depress breeding success, unless optimal arrival time has become later over recent years, which seems unlikely.

One possible cause of the apparent delay in pre-migratory fattening is energetic constraint, and several other lines of evidence suggest this may have been significant. Although moult and fattening periods overlap, there is little evidence for overlap at an individual level, suggesting that it may have been difficult to moult and fatten at the same time under the prevailing circumstances. That this is not always the case is shown by the frequency with which wagtails arrive on spring passage in Europe while moult is still in progress (Serra *et al.* 1992). Additionally, the occurrence of many birds at low weights in the population suggests that low-status birds, in particular females, were finding it difficult to maintain body condition.

The evidence converges on the conclusion that conditions encountered by the population at Nguru in 2005 were significantly worse than those enjoyed by populations studied previously at Kano and elsewhere through the period of pre-nuptial migration. One possibility is that low rainfall in the prior wet season could have caused low food availability, so that by the following March, towards the end of the dry season, food was even more scarce than usual. Only about 200 mm of rain fell in the Nguru area during the 2004 wet season, compared to 600–800 mm in an average year. However a similar low rainfall occurred in N Nigeria in the 1973 wet season, immediately prior to the first year of the Kano study, so this cannot explain the difference between the two sets of results.

If general weather and climatic conditions are not implicated, the cause may be found in conditions local to Nguru. The environment of the Hadejia-Jama'are floodplain has recently undergone profound changes, as a result of extensive silting and blockage of several major river channels. Consequent diversion of flow into the northern sector of the floodplain has led to catastrophic flooding, and the growth of stands of *Typha* covering huge areas. All of these factors have resulted in a dramatic shrinkage in the area under cultivation (Anon. 2005), which is the main foraging habitat used by Yellow Wagtails in the area. Such habitat loss could explain not only the delay in pre-migratory fattening, but also many of the other findings, including the densely-packed population, which may be the result of a historically large population being squeezed into a declining area of habitat over a relatively short timescale. The high level of aggression, seen particularly from territory-holding males, also fits with intense competition for shrinking resources.

The interpretation outlined above has implications for some fundamental aspects of the ecology of migrants during this critical phase of the annual cycle. The multiple signs of stress shown by the population provide circumstantial evidence for density dependent mortality in the form of poor body condition, and also possibly for lowered breeding success if delayed spring migration causes Nguru birds to lose out in competition for breeding territories with birds that have wintered elsewhere. This suggests that wagtails do not simply respond to loss of traditional wintering sites by moving elsewhere. If they did, population density would be expected to adjust rapidly, and there would be none of the social and physiological effects seen among the Nguru population. This in turn suggests that habitat loss in sub-Saharan wintering areas has the potential to contribute to overall population decline.

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