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Running Head: Conservation of declining migrants

The challenges of conservation for declining migrants: are reserve-based initiatives during the breeding season appropriate for the Pied Flycatcher *Ficedula hypoleuca*?

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Creating conservation policies for declining migrant species in response to global change presents a considerable challenge. Migrant species are affected by factors at breeding grounds, overwintering areas and during migration. Accordingly, reserve-based management during the breeding season is not always a suitable conservation strategy. Recent Pied Flycatcher population decline typifies the pattern for many migrants. The UK population has declined by 43% in the past decade, but explanations, and possible solutions, remain elusive. We use 15 years of data (1990-2004) from a declining British population to establish possible reasons for decline, considering: (1) breeding performance (including the influences of competition and predation); (2) weather patterns caused by the winter phase (December-March) of the North Atlantic Oscillation (NAO), which modify conditions experienced at wintering grounds and on migration; and (3) possible impacts of climate change on spring temperatures. We conclude that decreasing breeding performance is contributing to decline, but that non-breeding factors are more important. Winter NAO index is a strong predictor of breeding population, probably because it influences food abundance in Africa and at migratory stop-over points. Importantly; however, year itself enhances the predictive model, indicating that influences on population remain unaccounted for by current research. Management strategies based on increasing breeding productivity cannot fully address population decline because non-breeding factors appear important. However, as breeding performance is declining, breeding-based strategies remain useful conservation tools. To this end, our research indicates that optimal placement of nestboxes as regards orientation and habitat management to increase larval food supplies could increase productivity significantly.

Keywords: Breeding success, population dynamics, North Atlantic Oscillation (NAO),

Analysis of temporal change in population size, distribution and breeding success is important in ornithological research. Such identified changes can be both indicators of population trends and the effectiveness of management strategies (Wilson *et al*. 2005), thus providing valuable information for conservation at both local and global scales. Temporal change can also be indicative of widespread ecological change, particularly that relating to climate (Crick 2004). However, creating appropriate conservation policies for declining migrant species in response to global change presents a considerable challenge. Migrant birds are affected by factors acting at breeding grounds, overwintering areas and during migration. This geographical complexity not only makes establishing reasons for population decline difficult, but renders the development and implementation of conservation measures logistically challenging. Such problems are particularly pronounced for long-distance migrants such as the Pied Flycatcher *Ficedula hypoleuca*, the decline of which typifies the situation for many trans-Saharan species.

The quantification of population decline and investigation of possible causes, particularly with respect to productivity, can often be undertaken most effectively through intensive research at a single site as breeding parameters can be directly correlated with one another. Accordingly, intensive studies have been highlighted as a conservation priority, particularly for long-distance migrants (Amar *et al*. 2006, Holmes 2007). In the case of the Pied Flycatcher, decline in the British-breeding population of 20-43% is becoming increasingly well documented using data from the Repeat Woodland Bird Survey and the Breeding Bird Survey (Amar *et al*. 2006, Baillie *et al*. 2007), but explanations, and possible solutions, remain elusive. The comparative rarity of the species in the UK means that productivity trends are hard to determine from national studies. In this study, we analyse 15 years of data on Pied Flycatcher population and productivity from Nagshead RSPB Nature Reserve (Gloucestershire, UK) to investigate possible reasons for observed population decline in this species at a regionally important breeding site (Goodenough 2008a). We quantify temporal change in population size and productivity (direction and magnitude) and consider the interaction between these variables for the study population. We then test whether population decline can be better explained by factors at the breeding grounds (decreasing productivity, increasing competition or predation, changing temperatures) or factors external to the breeding grounds (weather patterns experienced at the wintering grounds or during migration resulting from the influence of the winter phase of the

North Atlantic Oscillation (NAO)) to help resolve the question of whether reserve based management during the breeding season is an effective conservation tool for this declining species. Finally, we discuss the practicalities of potential conservation strategies from a policy perspective.

METHODS

Study site

This study was undertaken at Nagshead Nature Reserve (Gloucestershire, UK), which covers 308 ha centred on 02°34’0”W, 51°47’0”N. The site supports a nationally important diversity of breeding birds and a regionally important Pied Flycatcher population. It is also home to the longest running nestbox scheme in the UK (Campbell 1968). Nestboxes are located primarily in a pre-1850 plantation of Pedunculate Oak *Quercus robur*, part of which is sheep-grazed.

Avian data

Data on nestbox occupations and breeding success of Pied Flycatchers at the Nagshead Reserve during the period 1990-2004 were obtained from the Royal Society for the Protection of Birds (RSPB) who manage the site. Data from 295 wooden nestboxes suitable for Pied Flycatcher occupation (rectangular with a sloping roof; approximate internal measurements: 110 mm width, 170 mm depth, 210 mm mid-point height), and which had been available throughout the entire period, were included in the study. This gave a total of 732 breeding attempts (of which 722 had a known outcome) after removal of seven known relaying attempts, all of which were unsuccessful. It should be noted that six nestboxes on the reserve that were suitable for Pied Flycatchers were excluded from the study as they were not monitored routinely by nestbox checkers. Any potential bias of this exclusion on population or productivity estimates would have been be extremely slight. Mean annual nestbox occupation by all hole-nesting passerines was 73% (range 61-90%). Breeding success data comprised three absolute measures of breeding success (clutch size, number hatched and number fledged). Two relative success measures (the proportion of eggs hatched and the proportion of young fledged) were calculated from the available data. As fledging was witnessed on very few occasions, fledging was deemed to have occurred when the young birds were capable of leaving the nest on one visit and, on the subsequent visit, the nest was found empty and undisturbed with a well-trodden lining containing feather scale and droppings (Beaven & Leech 2003). Any dead or injured young that remained in the nestbox after fledging were deducted from the number of young recorded as fledged.

Because Pied Flycatchers use nestboxes in preference to natural cavities, a surplus of nestboxes enabled the breeding of (almost) all individuals within the population to be accounted for, such that nestbox occupations were a reliable proxy for breeding population size. In addition, because nests were recorded at the nest-building stage and were monitored throughout, data could be analysed without using the Mayfield method and the simplifying assumptions therein (Mayfield 1975, Hensler & Nichols 1981).

Statistical analyses

Count data were log (*ln*+1) transformed and proportional data were arcsine square root transformed to achieve normality. Statistics were undertaken using SPSS for Windows 14.0. To analyse temporal changes in the size of the breeding population, bivariate regression was used with year as the predictor variable. The same approach was used to test for temporal change in productivity, with the additional use of Bonferroni probability value adjustments to allow for multiple calculations. To analyse temporal change in productivity, unweighted annual means were calculated for each parameter to mitigate pseudoreplication problems. To determine whether within-year variability in breeding success changed significantly between 1990 and 2004, the interquartile range (IQR) of each breeding success parameter was calculated on a yearly basis and regressed against year. IQR was chosen as the variability measure since this quantifies the success of the most typical 50% of broods. This excluded outliers and reduced the bias from atypical years which have skewed breeding success parameters (Lundberg and Alatalo, 1992). Change in complete nest failure was analysed by calculating a binary success/failure variable for each nest (0 = no young fledged; 1 = at least one young fledged) and entering this as the dependent variable in a logistic regression analysis. This analysis was undertaken on the whole dataset.

To establish what annually variable factors, other than year itself, might influence the breeding population, exploratory stepwise multiple linear regression (MLR) analysis (entry criterion α =

0.05; subsequent removal criterion α= 0.10; Field 2000) was used with the number of nestbox occupations per year as the dependent variable. Five predictor variables were available for entry into the MLR analyses, describing: (1) competition (nestbox occupations by heterospecifics); (2) past productivity (mean number of young fledged per brood the preceding season); and (3, 4, 5) temperature (mean temperatures for April, May, June respectively). The above variables were identified using *a priori* knowledge (see below for rationale):

- Nest site competition: a known influence on breeding population and annually variable at the site, with percentage of nestboxes occupied by heterospecifics ranging from 51% (1999) to 81% (2003).
- Fledging success the preceding season can affect recruitment into the breeding population as previously determined for Pied Flycatchers in Finland (Virolainen 1984). The average number of young fledged was quantified using the mean (rather than the median) as: (1) it allowed results to be directly compared with those of Virolainen (1984); and (2) the median is restricted to integer and .5 values which, in the study of the fledging success in a small passerine, lacks precision and gives a very few possible values such that the validity of using regression to analyse data is unsatisfactory.
- Spring temperature: a fundamental influence on all aspects of avian breeding, including breeding density (Sæther *et al*. 2004). The temperature data were collected from the nearest Meteorological Office weather station (Ross-on-Wye, Herefordshire, eight miles north of Nagshead). The proximity of the weather station to the study site, the similar altitudes, and the use of monthly averages rather than daily readings, justifies the use of off-site data in this study (Perrins 1991). Having three temperature measures exceeded the case:variable ratio beyond that recommended for MLR (Tabachnick & Fidell 1989) and confounded the multicollinearity assumption. Accordingly, only one temperature variable was made available for entry into an analysis at any one time (Elliot *et al*. 2000).

One problem with ecological modelling is the lack of validation of models, particularly the lack of the most rigorous form of validation: prediction of values and comparison with new field data (McGarigal *et al*. 2000). This can be a specific problem in stepwise procedures due to elevated r^2 values that can render the predictive accuracy of the model uncertain in the absence of cross-validation (Whittingham *et al*. 2006). Here, MLR models were cross-validated by making predictions for the 2006 and 2007 breeding seasons and comparing these to primary field data to ensure that the model, and the research results arising from its use, were sound. All models generated were used to draw inferences, rather than restricting consideration to the minimum adequate model. To ensure that regression analyses were used appropriately, assumptions of normality, linearity, homoscedasticity and autocorrelation were assessed by examining residual plots and using Shapiro-Wilk and Durbin-Watson tests (Shaw 2003). The assumption of a lack of multicollinearity was tested for MLR analyses using tolerance collinearity statistics (Field 2000). The variance explained by any MLR regression was calculated using the adjusted r^2 to avoid the number of independent variables biasing the model.

RESULTS

Temporal change in breeding population

The number of Pied Flycatcher nests per year has declined severely, falling from 86 in 1990 to just 23 in 2004 (Fig. 1). This is a decrease of 73.3% or 4.2 nests per year ($r = -0.93$, $n = 15$, $P < 0.001$), and as nestbox occupations are a good proxy for breeding population (see above), it suggests the reserve's breeding population is undergoing severe decline.

Temporal change in productivity

Breeding success decreased by 0.17 fledglings per brood per year, while the proportion of fledglings per brood decreased by 31.80% in total between 1990 and 2004. Clutch size, number hatched and the proportion of eggs hatched per clutch remained stable (Table 1). The mean clutch size per year over the period 1990-2004 (6.67 ± 0.38 sd based on 712 nests in 15 years) was significantly lower than the mean clutch size during 1948-1963 (6.97 ± 0.32 sd based on 1,131 nests in 16 years: calculated from Lack 1966) at the same study site (independent two-sample *t*-test, $t = 2.07$, df = 29, $P = 0.048$). This last point should be interpreted cautiously as the method used to exclude relaying attempts in Lack's study (arbitrary removal of late clutches) might have resulted in some genuine late (thus small) clutches being excluded from the 1948-1963 dataset. The nest failure rate (most usually due to whole-brood predation or desertion) remained statistically constant ($ß = -0.04$, $n = 722$, $P = 0.079$) although the borderline-significant result indicates there was some reduction in nest failures during the study period that might be biologically significant. This interpretation was supported by an effect size (calculated using the odds ratio method) of < 1 (exp ß = 0.96), suggesting a potentially important reduction in total nest loss. When additional analyses were run for number fledged and proportion fledged from successful nests only to establish the pure temporal trend in partial losses, the decrease in breeding success became more dramatic than when total and partial losses were confounded (Table 1; Fig. 2). There was no change in within-year variability of any measure of breeding success during the 15-year period ($P > 0.2$; tests not shown).

Exploratory analysis

Stepwise MLR analysis to explain temporal change in Pied Flycatcher breeding density, as defined by the number of nestbox occupations (this factor being entered as the dependent variable), resulted in three initial models being constructed. Year was entered into the first model, mean number of young fledged per brood the preceding season was added to create a second model, and finally mean April temperature was added to create a third model (Table 2). The third model explained 94.7% of variance in the size of the Pied Flycatcher breeding population. Although there was some multicollinearity in the second and third models due to the correlation of year with breeding success the preceding year, collinearity statistics (see above) showed that this was well within limits, such that the model was not compromised. Hierarchical MLR (whereby the mean number of young fledged the previous year was entered before year) confirmed that year had a significant effect on the Pied Flycatcher breeding population over and above that caused by its influence on fledging success the preceding season. On its own, the mean number of young fledged the preceding season explained 36.7% of variance in the Pied Flycatcher population size (Fig. 3a). This was also supported by a significant relationship between mean number of young fledged the previous year and annual percentage change in population size ($r = 0.56$, $n = 14$, $P = 0.037$; Fig.3b). Competition (nestbox occupations by heterospecifics) was not included as a significant predictor in any model.

Because Pied Flycatchers are migratory and most individuals do not reach the breeding grounds until mid- to late- April, it seemed unlikely that mean April temperatures *per se* could influence the size of the breeding population, especially as most variability occurred in the first half of the month. The possibility that more migrant returnees were able to recruit into the breeding population when colder April temperatures delayed leaf burst and caterpillar emergence at the breeding grounds, such that any phenological mismatch was reduced (Both & Visser 2001), was rejected as the relationship between breeding population size and temperature was positive, not negative. As April temperature did not influence the size of co-occurring resident species' populations at the same site (Goodenough 2008a), the possibility of it being a proxy for migratory conditions was considered. Spring temperatures in the UK often correlate with the winter North Atlantic Oscillation (NAO) index (Qian & Saunders 2003), which has previously been associated with avian population dynamics (Sæther e*t al*. 2004). Accordingly, April temperatures for the study area were correlated with NAO data for the preceding winter (December-March). These data quantified the differences in barometric air pressure between Stykkisholmur (Iceland) and Gibraltar associated with variation in winter and spring weather patterns of Europe and North Africa (Jones *et al*. 1997, Osborn 2006) and were obtained from the University of East Anglia (http://www.cru.uea.ac.uk/ftpdata/nao.dat and http://www.cru.uea.ac.uk/~timo/projpages/nao-update.htm). A persuasive, but non-significant, negative correlation was found between winter NAO data and April temperatures at the study site (r = -0.45, n = 15, P = 0.096). To establish if more variance in the size of the Pied Flycatcher breeding population was explained using winter NAO rather than April temperature as a predictor, the latter was replaced with the former in the MLR candidate variable list. The winter NAO index was found to be a significant predictor of breeding population size, being entered into the MLR at the same place as April temperature had been previously. Moreover, the variance explained by the resultant model increased from 94.7% to 96.2%. Cross-validation showed that this final model (year, previous breeding success and winter NAO index) could be used predictively with very high accuracy: the prediction of population size in the 2006 breeding season was 97.8% accurate (Table 2), while prediction of the 2007 population was 96.5% accurate. In both cases, the accuracy of the actual prediction was higher than the calculated r^2 value.

The absence of a relationship between the overall density of nestbox breeding birds (nestbox occupations by all heterospecifics) and the size of the Pied Flycatcher breeding population was suggested by the exclusion of the density predictor variable in all MLR models (see above). This was verified by checking for species-specific relationships between the Pied Flycatcher population and that of the other common Nagshead nestbox occupants (Pearson correlation between Pied Flycatcher and Blue Tit *Cyanistes caeruleus* r = -0.36, n = 15, P = 0.185; between Pied Flycatcher and Great Tit *Parus major* r = 0.13, n = 15, P = 0.639).

DISCUSSION

Temporal change in breeding population

The decrease in the Pied Flycatcher breeding population at Nagshead of 73% (1990-2004) is much greater than that shown nationally: BBS data showed a 43% decline (1995-2005) while the Repeat Woodland Bird Survey found a 20-25% decline (1980s-2003/4) (Amar *et al*. 2006, Baillie *et al*. 2007). The disparity between the Nagshead population and the national trend may be because the national studies were skewed towards the more stable Welsh population. Although the severe decline reported here might be site-specific, it could be indicative of range contraction or future decline, especially as the study site is on the eastern limit of the species' range in southern Britain (Gibbons *et al*. 1993). Crucially, if the decline of 73% were reflected across the UK, the species would more than meet the 50% decline criterion for red-listing as a species of high conservation concern (Gregory *et al*. 2002). Decline in Pied Flycatcher populations is not limited to the UK, and is also occurring in other areas of Europe (e.g. Both *et al*. 2006).

Temporal change in productivity

The only breeding success parameters to change over time were the number and proportion of young fledged per brood. Quantification of change in productivity is important as the comparative rarity of the species in the UK means that national trends cannot be reliably determined from national studies such as the Nest Record Scheme (NRS) or from ringing at Constant Effort Sites (CES). The number of nest failures as a proportion of the total number of nests decreased (non-significant result but the effect size is large indicating that this could be biologically, if not statistically, significant). This indicates that the decrease in breeding success is not a result of more total nest failures (which are usually due to predation or desertion). This is reassuring as there have been concerns about the impact of increasing Grey Squirrel *Sciurus carolinensis* numbers on breeding success (Siriwardena 2004) given the detrimental effects of non-native predators on reproduction in other species (Goodenough 2008b). Partial losses, on the other hand, have increased at a very high rate. The most likely candidate factor for a systematic and substantial decrease in partial nesting success (i.e. reduced nestling survival) is a change in food resources, particularly in the caterpillar food supply so important for chicks (Perrins 1991). Unfortunately, there are no data on food availability at Nagshead, but anecdotal evidence from site-based RSPB staff (I. Proctor pers. comm.) suggests that this might be a problem, especially given the lepidopteran declines observed both locally (Gaunt 2005) and nationally (Harding 2002, Conrad *et al*. 2004) and the fact that other birds such as Blue Tits and Great Tits are also suffering reduced productivity at the study site (Goodenough 2008a). Food shortages could also result from phenological mismatches between breeding and peak food supply (Both *et al*. 2006).

Exploratory analysis

The importance that the mean number of young fledged per brood the previous year has on the size of the Pied Flycatcher breeding population is in accordance with research by Virolainen (1984) on a breeding population at Lake Kimpari in Finland. However, the relationship between these variables at Nagshead was not as strong as that at Lake Kimpari, even though the similar-sized populations were both declining. This reflects spatial variation in population dynamics, even between apparently similar populations. Similarly, Stenning (1984) showed a strong relationship between the post-breeding size of the Nagshead Pied Flycatcher population in one year (which would be strongly correlated with fledging success in that year) and the breeding population the following year (57% of variance explained, increasing to 76% after controlling for the influence of immigration).

The relationship between winter NAO index and breeding population size is important as it is notoriously difficult to establish the influence of factors external to the breeding ground on breeding for migrant species (Newton 2004). The relationship between the size of the breeding population and NAO was negative, such that there were more nestbox occupations in a low-NAO year than in a high-NAO year. Low (negative) NAO years are associated with higher precipitation in the Sahel region and in Southern Europe which results in more vegetation and higher insect abundance (Rodó *et al*. 1997, Gemmill 2005, Chen & Wang 2007). Insect abundances in the Sahel and in stop-over areas in Spain and Portugal are likely to have a considerable impact on winter and migratory survival (Bibby & Green 1980, Newton 2006). This parallels the situation for two other trans-Saharan migrants: low NAO index is associated with a higher return rate of White Storks *Ciconia ciconia* and adult Common Terns *Sterna hirundo* to their European breeding grounds (Sæther *et al*. 2006, Favero & Becker 2006). Previous studies on the NAO (and the El Niño Southern Oscillation (ENSO) in the southern hemisphere) have revealed correlations with migratory phenology (Forchhammer *et al*. 2002, Hubálek 2003), breeding phenology (Forchhammer *et al*. 1998, Wilson & Arcese 2003) and breeding success (Nott *et al*. 2002, Sanz 2003). However, comparatively few studies have related migratory and winter survival to these large-scale weather patterns. The relationship between these variables for the Pied Flycatcher is, therefore, important evidence that climatic conditions outside the breeding season can be a fundamental influence on the population dynamics of a migratory passerine. Interestingly, a previous study that examined fluctuations in Pied Flycatcher populations on a pan-European scale and correlated this to NAO data (Sæther *et al*. 2003) included the study site during the period 1948-1963 (using data published in Stenning *et al*. 1988) but found no significant relationship for this population (B-E Sæther pers. comm.). This might suggest that recent change in the NAO weather patterns is increasing the influence of global weather systems on population dynamics. The 1990-2004 Nagshead data also indicate that the NAO index, when combined with other population variables, can be used predictively as well as explain residual variation in population dynamics (e.g. Stokke *et al*. 2005). However, such analysis requires detailed information as response to NAO is population-specific (Sæther *et al*. 2003).

Importantly, although the mean number of young fledged per brood the preceding season and winter NAO are significant predictors of Pied Flycatcher population size, year itself still enhances the model, indicating that other influences on population size remain unexplained. One possibility worthy of further study is a possible increasing lack of synchrony between birds and their caterpillar food supply (Both & Visser 2001). Whereas resident species such as Blue Tits are advancing their lay date at the same study site (Goodenough 2008a), Pied Flycatcher lay dates have remained the same at Nagshead since 1948 (Lack 1966, Goodenough 2008a), possibly as individuals are constrained in phenological adjustment by their migratory strategy. De-coupling has already been seen in Pied Flycatcher populations in the Netherlands where response to warmer temperatures has differed across trophic levels (entomological and ornithological) resulting in a phenological mismatch and population declines of up to 90% (Both *et al*. 2006).

Conservation implications

The declining breeding population and decreasing breeding success are of significant conservation concern. The decrease in fledging success appears to be partly responsible for the reduction in the size of the breeding population in subsequent years, but other factors are likely to be involved. This is typical for declining long-distance migrant species when a complex series of interacting factors throughout the yearly cycle at wintering and breeding grounds and on migration can combine to cause decline (Newton 2004; Fig. 4). One possibility for further study is to compare population dynamics of Pied Flycatchers and Collared Flycatchers *Ficedula albicollis.* As these closely related species winter sympatrically in countries such as Chad and Nigeria (Dowsett 1993, Elgood *et al.* 1994) but breed allopatrically, use of the comparative approach may enable the primary influences on population to be disentangled. Specific Pied Flycatcher breeding populations have particular wintering areas and migratory routes (Hope-Jones *et al.* 1977) and may thus be influenced by site-specific factors other than those at their breeding grounds. This could explain why some British-breeding populations are decreasing while others are not, when there is no (apparent) difference in the quality of their breeding areas.

The ecological complexity of migratory species means that factors causing decline cannot always be satisfactorily addressed in breeding areas (Freeman & Crick 2003). In the case of the Pied Flycatcher, management strategies directed to increasing breeding productivity cannot address all aspects of population decline since non-breeding factors appear important. However, measures that increase breeding productivity should help reduce the decline. Previous research (Goodenough 2008a) has shown that nestboxes facing southwest are associated with decreased Pied Flycatcher nestling survival, but that birds still use boxes of this orientation. Thus it might be to advantage if boxes are oriented in an arc from west through north to south to force the choice of suitable nest sites. Habitat management to create and maintain a good diversity of lepidopteran host plants may also be useful if a decrease in caterpillar food supply is indeed reducing productivity.

Further research is needed to determine which factors external to the breeding site may be causing decline. Such research will require multinational cooperation and needs to consider changes in both the abiotic and biotic environments. Specific targets for research include migratory stop-over locations, particularly where Cork Oak plantations are felled, and key wintering sites where changes in management might be impacting upon food supplies (Newton 2006). It is only when the causes of decline are fully understood throughout migratory cycles that maximally effective integrated conservation strategies for declining migrants, such as the Pied Flycatcher, can be achieved.

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Table 1: Temporal trends in Pied Flycatcher breeding success at Nagshead (1990-2004; *n* = 15 years). Calculations were performed on unweighted annual mean count data (log-transformed) or proportional data (arcsine square root transformed) with the figure for slope back-transformed to aid interpretation. Analyses of proportional success were undertaken to disentangle whether year was affecting later stages of breeding success solely because of its influence on earlier stages of nesting, or in addition to this earlier influence. Analysis of successful nests (defined as those from which at least one young fledged) show change in partial nest failure.

Dependent Variable	**Slope**	r^2	***P****
Clutch size	-0.019	0.05	0.421
Number hatched	-0.016	0.02	0.624
Number fledged	-0.173	0.31	0.032
Proportion hatched	0.120	< 0.01	0.815
Proportion fledged	-2.469	0.32	0.029
Number fledged from successful nests	-0.182	0.37	0.015
Proportion fledged from successful nests	-2.680	0.43	0.008

* The significance of the *P* values remained unaltered when Bonferroni corrections were applied to account for the non-independence of the dependant variables.

Table 2. Independent variables that explain variation in the size of the Nagshead Pied Flycatcher breeding population. Population was determined using nestbox occupations in 1990-2004 as a proxy dependent variable and analysed using stepwise multiple linear regression, which created four models based on the number of independent variables entered (*n* = 15 years).

Model	**Variables**	**Linear equation**	***r*² ***	***P***	**2006 Breeding Population ≠**	
					Predicted number of pairs	**Prediction accuracy (actual number of pairs = 23)**
1	Year (x)	$y = -4.002x + 8024.010$	0.84	< 0.001	18.99	78.9%
2	Year (x_1) + Mean number to fledge the preceding season (x_2)	$y = -3.508x_1 + 4.414x_2 + 7033.629$	0.93	< 0.001	20.59	88.3%
3	Year (x_1) + Mean number to fledge the preceding season (x_2) + Mean April temperature (x_3)	$y = -3.890x_1 + 3.435x_2 + 3.455x_3 + 7754.313$	0.95	< 0.001	19.00	79.0%
4	Year (x_1) + Mean number to fledge the preceding season (x_2) + Winter (Dec.-Mar.) North Atlantic Oscillation Index (x_3)	$y = -3.786x_1 + 4.178x_2 + -2.172x_3 + 7592.602$	0.96	< 0.001	22.50	97.8%

* The r^2 value was adjusted (see text) when more than one independent variable was entered into a model.

≠ Models were cross-validated by using them to predict the breeding population in 2006 and comparing this to actual data based on field observations (23 breeding attempts). Further validation was undertaken on the 2007 breeding population, when prediction was 96.5% accurate using model 4, substantially higher than the next best (model 3) at 88% (calculations not shown).

FIGURE LEGENDS

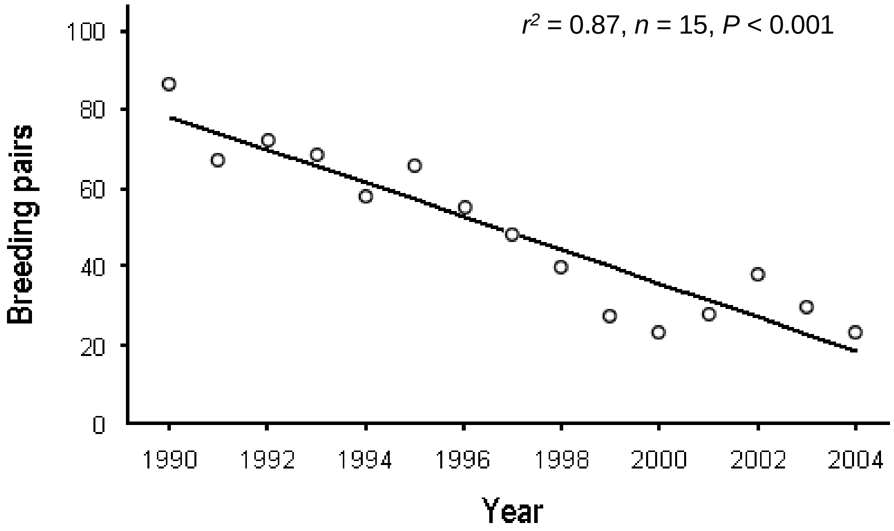
Figure 1. Temporal change in the number of breeding pairs of Pied Flycatchers (as determined by number of occupations in a static resource of 295 nestboxes) at Nagshead between 1990 and 2004.

Figure 2. The relationship between year and the percentage of young fledged per brood from successful nests (defined as nests where at least one young fledged).

Figure 3. The relationship between the size of the Pied Flycatcher breeding population and the mean number of young fledged per brood the previous year in terms of: (a) absolute population size in a given year; and (b) relative annual change in population from the previous year.

Figure 4. Summary of the factors that can influence population dynamics in migratory species such as the Pied Flycatcher. The species cannot be reserve dependent owing to the wide spatial coverage inherent in a trans-Saharan migrant.

Figure 1



$r^2 = 0.87$, $n = 15$, $P < 0.001$

Figure 2

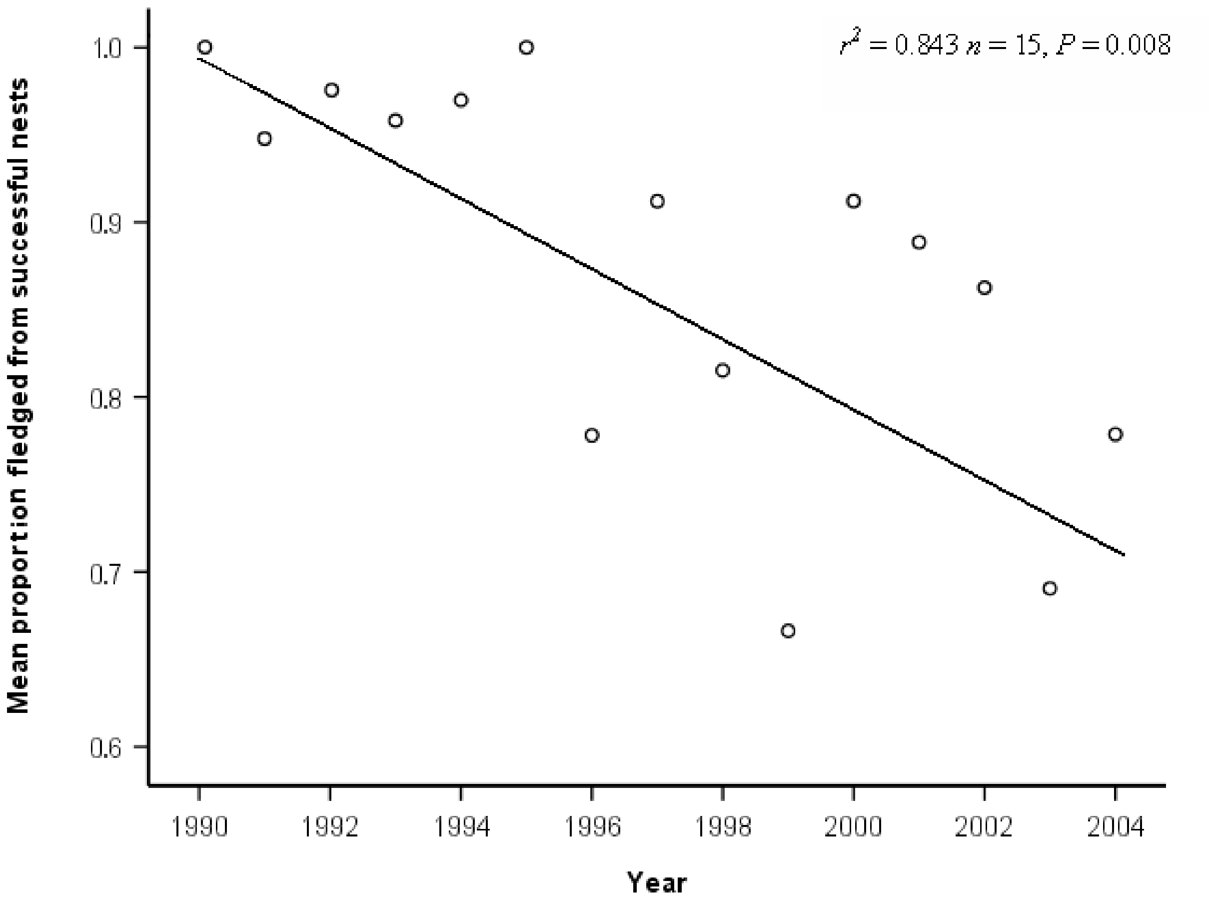

$r^2 = 0.843$ $n = 15$, $P = 0.008$
Mean proportion fledged from successful nests
1.0
0.9
0.8
0.7
0.6
1990
1992
1994
1996
1998
2000
2002
2004
Year

Figure 3

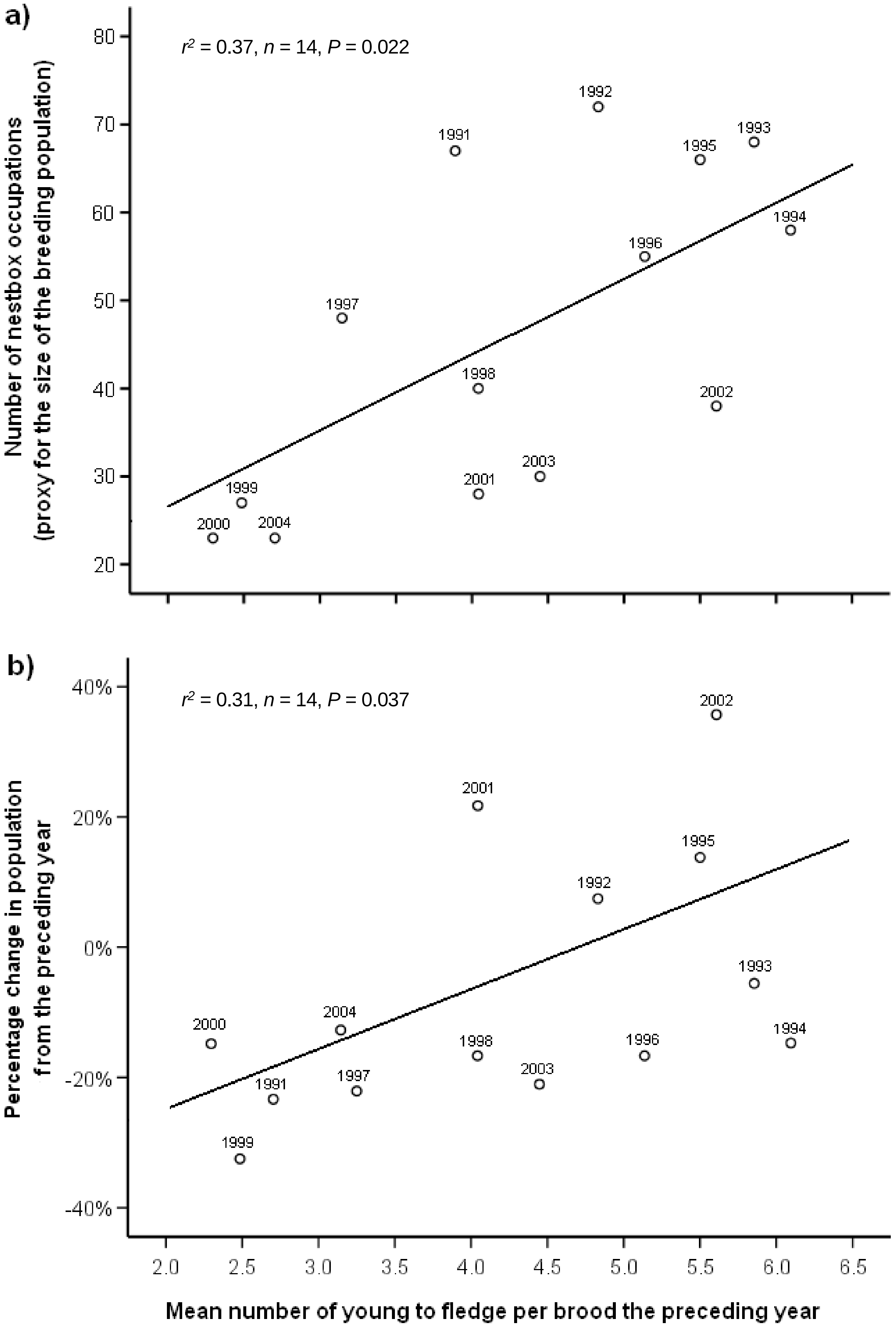
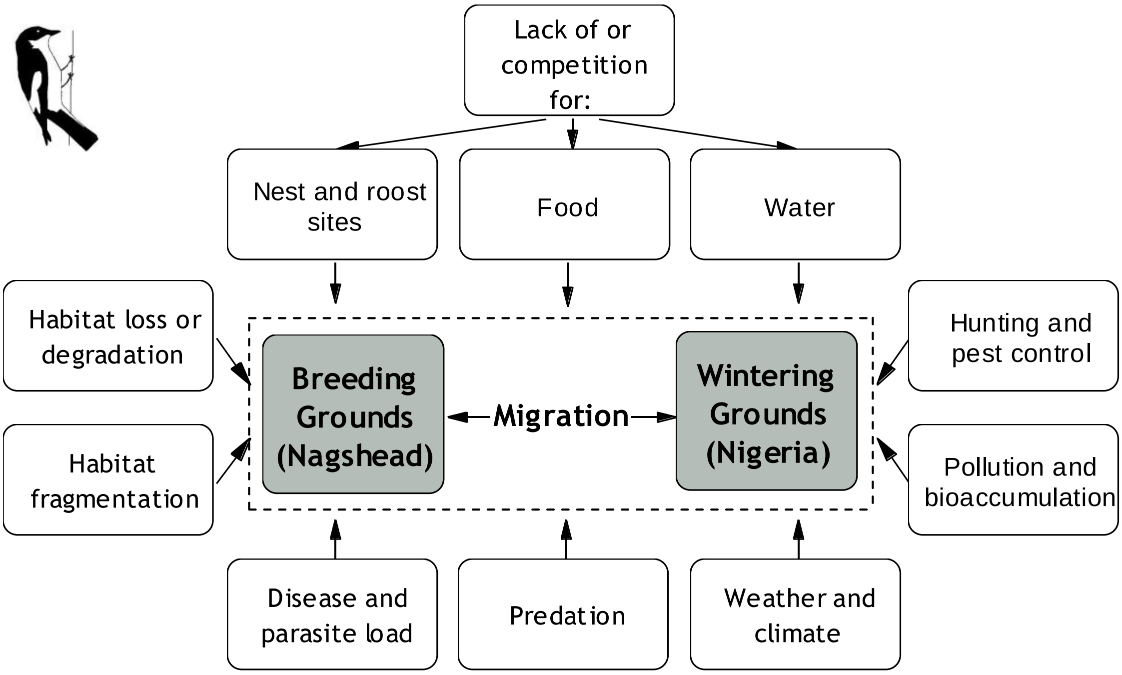

a)
$r^2 = 0.37$, $n = 14$, $P = 0.022$
Number of nestbox occupations
(proxy for the size of the breeding population)
80
70
60
50
40
30
20
1992
1991
1995
1993
1994
1996
1997
1998
2002
2003
2001
1999
2000
2004
b)
$r^2 = 0.31$, $n = 14$, $P = 0.037$
Percentage change in population
from the preceding year
40%
20%
0%
-20%
-40%
2002
2001
1995
1992
1993
2000
2004
1998
1996
1994
2003
1991
1997
1999
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
Mean number of young to fledge per brood the preceding year

Figure 4


Lack of or competition for:
Nest and roost sites
Food
Water
Habitat loss or degradation
Habitat fragmentation
Breeding Grounds (Nagshead)
Migration
Wintering Grounds (Nigeria)
Hunting and pest control
Pollution and bioaccumulation
Disease and parasite load
Predation
Weather and climate