



Review article

The decline of Afro-Palaeartic migrants and an assessment of potential causes

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There is compelling evidence that Afro-Palaeartic (A-P) migrant bird populations have declined in Europe in recent decades, often to a greater degree than resident or short-distance migrants. There appear to have been two phases of decline. The first in the 1960s–1970s, and in some cases into the early 1980s, largely affected species wintering predominantly in the arid Sahelian zone, and the second since the 1980s has mostly affected species wintering in the humid tropics and Guinea forest zone. Potential drivers of these declines are diverse and are spread across and interact within the migratory cycle. Our knowledge of declining species is generally better for the breeding than the non-breeding parts of their life cycles, but there are significant gaps in both for many species. On the breeding grounds, degradation of breeding habitats is the factor affecting the demography of the largest number of species, particularly within agricultural systems and woodland and forests. In the non-breeding areas, the interacting factors of anthropogenic habitat degradation and climatic conditions, particularly drought in the Sahel zone, appear to be the most important factors. Based on our synthesis of existing information, we suggest four priorities for further research: (1) use of new and emerging tracking technologies to identify migratory pathways and strategies, understand migratory connectivity and enable field research to be targeted more effectively; (2) undertake detailed field studies in sub-Saharan Africa and at staging sites, where we understand little about distribution patterns, habitat use and foraging ecology; (3) make better use of the wealth of data from the European breeding grounds to explore spatial and temporal patterns in demographic parameters and relate these to migratory pathways and large-scale patterns of habitat change and climatic factors; and (4) make better use of remote sensing to improve our understanding of how and where land cover is changing across these extensive areas and how this impacts A-P migrants. This research needs to inform and underpin a flyway approach to conservation, evaluating a suite of drivers across the migratory cycle and combining this with an understanding of land management practices that integrate the needs of birds and people in these areas.

Keywords: breeding and wintering grounds, drivers of change, migration, population trends, staging sites.

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There is growing evidence that Afro-Palaeartic (A-P) migrants are in decline throughout Europe, with declines often being more pronounced than those of either short-distance migrants or sedentary species (Sanderson *et al.* 2006, Heldbjerg & Fox

2008, Thaxter *et al.* 2010). These declines are of growing conservation concern in both scientific and political arenas (e.g. http://www.cms.int/bodies/COP/cop10/resolutions_adopted/10_27_landbirds_e.pdf), as the European breeding populations of some formerly widespread species, such as Ortolan Bunting *Emberiza hortulana*, European Turtle Dove *Streptopelia turtur*, Whinchat *Saxicola rubetra*, Northern Wheatear *Oenanthe oenanthe* and Nightingale *Luscinia megarhynchos*, have more than halved over 30 years (Table 1).

Migrant birds are likely to be more susceptible to environmental change than their resident counterparts, as their complex annual cycle, long migration routes and dependence on different sites at different times place them in 'multiple jeopardy' (Newton 2004a). However, despite the large number of A-P migrants in decline, there have been few attempts to review the evidence for the factors underlying these patterns, with the exception of Zwarts *et al.* (2009), who focused in particular on the Sahelian region.

This review provides a synthesis of evidence for the extent to which different factors are responsible for driving the declines of A-P migrants in the breeding and non-breeding (wintering and staging) areas, focusing on European-breeding species. The review falls into four sections. First, we summarize information on the nature and extent of declines using trend data collected on breeding populations across Europe. Secondly, we review the nature and strength of the evidence for an impact of different factors in driving the declines. Thirdly, we look in detail at the drivers of change. Fourthly, we attempt to identify the most important research gaps that need to be addressed to underpin the future conservation of these species.

POPULATION TRENDS OF AFRO-PALAEARCTIC MIGRANTS

An A-P migrant is a species in which at least part of the population moves between breeding areas in the Palaearctic region and non-breeding grounds in sub-Saharan Africa each year (Moreau 1972, Berthold 2001, Newton 2004a). Under the widely recognized classification of migratory strategy outlined by BirdLife International (2004), 126 bird species are regarded as A-P migrants, with estimates of the overall numbers of individual birds involved ranging from 2.1 billion (Hahn *et al.* 2009) to more than 5 billion (Moreau 1972).

Table 1. Long-term (1980–2009) population trends of selected European Afro-Palaearctic migrants covered by the Pan-European Common Bird Monitoring Scheme (PECBMS), in order of magnitude of decline. Trends are derived from the combined breeding bird surveys of the following 25 countries: Austria, Belgium, Bulgaria, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, The Netherlands, Norway, Poland, Portugal, Slovenia, Slovakia, Spain, Sweden, Switzerland and UK.

Species	Long-term Pan-European trend (%)	Mean annual rate of change (%)
Ortolan Bunting <i>Emberiza hortulana</i>	-84	-6.12
European Turtle Dove <i>Streptopelia turtur</i>	-69	-3.96
Whinchat <i>Saxicola rubetra</i>	-67	-3.75
Northern Wheatear <i>Oenanthe oenanthe</i>	-66	-3.65
Common Nightingale <i>Luscinia megarhynchos</i>	-63	-3.37
River Warbler <i>Locustella fluviatilis</i> ^a	-62	-3.28
Tree Pipit <i>Anthus trivialis</i>	-54	-2.64
Yellow Wagtail <i>Motacilla flava</i>	-53	-2.57
Icterine Warbler <i>Hippolais icterina</i>	-50	-2.36
Eurasian Wryneck <i>Jynx torquilla</i>	-49	-2.30
Barred Warbler <i>Sylvia nisoria</i> ^a	-48	-2.23
Black-tailed Godwit <i>Limosa limosa</i>	-45	-2.04
Spotted Flycatcher <i>Muscicapa striata</i>	-43	-1.92
Common Grasshopper Warbler <i>Locustella naevia</i>	-39	-1.69
Red-backed Shrike <i>Lanius collurio</i>	-36	-1.53
Wood Warbler <i>Phylloscopus sibilatrix</i>	-33	-1.37
Willow Warbler <i>Phylloscopus trochilis</i>	-33	-1.37
Whimbrel <i>Numenius phaeopus</i>	-28	-1.13
Garden Warbler <i>Sylvia borin</i>	-25	-0.99
Common Sandpiper <i>Actitis hypoleucos</i>	-21	-0.81
Common Cuckoo <i>Cuculus canorus</i>	-21	-0.81
Pied Flycatcher <i>Ficedula hypoleuca</i>	-21	-0.81
House Martin <i>Delichon urbica</i>	-18	-0.68
Barn Swallow <i>Hirundo rustica</i>	-18	-0.68

(continued)

Table 1. (continued)

Species	Long-term Pan-European trend (%)	Mean annual rate of change (%)
Lesser Whitethroat <i>Sylvia curruca</i>	-15	-0.56
Sedge Warbler <i>Acrocephalus schoenobaenus</i>	-12	-0.44
Eurasian Reed Warbler <i>Acrocephalus scirpaceus</i>	-7	-0.25
Common Swift <i>Apus apus</i>	5	0.17
Common Redstart <i>Phoenicurus phoenicurus</i>	7	0.23
Thrush Nightingale <i>Luscinia luscinia</i>	9	0.30
Marsh Warbler <i>Acrocephalus palustris</i>	15	0.48
Eurasian Golden Oriole <i>Oriolus oriolus</i>	18	0.57
Great Reed Warbler <i>Acrocephalus arundinaceus</i> ^a	20	0.63
Common Whitethroat <i>Sylvia communis</i>	27	0.83
Hoopoe <i>Upupa epops</i> ^a	137	3.02
Collared Flycatcher <i>Ficedula albicollis</i> ^a	142	3.09
White Stork <i>Ciconia ciconia</i> ^a	204	3.91
Marsh Harrier <i>Circus aeruginosus</i>	310	4.99

^aData only available for the period 1982–2009.

Analyses of long-term datasets on the international (European) and national (individual countries within Europe) scales have shown that A-P migrants are in decline. Although these data tend to be biased towards Western Europe, they suggest widescale, long-term declines across a broad range of species. The aggregate population trajectory of long-distance migrants in Europe derived from the Pan-European Common Bird Monitoring Scheme (PECBMS: <http://www.ebcc.info/pecbm.html>), which covers a selection of commoner land birds, declined by 23% between 1980 and 2009, whereas that for residents and short-distance migrants combined declined by just 7% (Fig. 1a: $F_{1,29} = 19.03$, $P < 0.001$). Of the 38 widespread A-P migrants monitored by this scheme since 1980, 27 (71%) have declined in abundance and 11 (29%) have increased (Table 1). Trends in residents and migrants were similar from 1980 to 1990, but from that point they diverge. At a national level, population trends of A-P migrants in several European countries and regions also

showed declines that exceeded those of short-distance migrants and residents (e.g. Denmark, Heldbjerg & Fox 2008; Germany, Flade *et al.* 2008; The Netherlands, Van Turnhout *et al.* 2010a), although this difference was not evident in three countries (France, Julliard *et al.* 2003; Estonia, Kuresoo *et al.* 2011; Czech Republic, Reif *et al.* 2010). If we divide the long-distance migrants monitored by the PECBMS into those associated with farmland and those in other habitats, and examine their grouped-species trends, there is a suggestion that farmland migrants have fared worse than the others, but the trends are not significantly different (Fig. 1b: $F_{1,29} = 3.92$, $P = 0.058$).

Examination of long-term datasets in Europe reveals two relatively distinct periods of decline that are broadly consistent between studies and are evident on both national and European scales. At the European level, two studies using data from the *Birds in Europe (BiE)* database (BirdLife International 2004) show that A-P migrants declined markedly in Europe during 1970–1990, but less so between 1990 and 2000 (Sanderson *et al.* 2006, Møller *et al.* 2008). Of the 119 species considered, 40 (33%) declined significantly and 15 increased between 1970 and 1990, whereas between 1990 and 2000, numbers of increasing and decreasing migrants were similar (20 and 18, respectively; Sanderson *et al.* 2006). The greatest declines between 1970 and 1990 were among birds that winter in open savannahs and breed on agricultural land (Sanderson *et al.* 2006). Population trend data from the PECBMS for widespread European birds over three decades show that A-P migrants that predominantly winter in arid northern areas show significantly different trends from those that winter in the humid southern areas in Africa (Fig. 1c: $F_{1,29} = 6.03$, $P = 0.021$). The latter group declined consistently from 1980, whereas the former showed a sharp decline from 1980 to 1994 (c. 36%) but then an increasing trend from 1995 to 2009 (c. 14%), suggesting a partial recovery of some species.

This apparent divergence in trends between species wintering in arid and humid zones was first shown by Hewson and Noble (2009) and was confirmed, for a wider group of species and over a longer time scale, by Thaxter *et al.* (2010) using population data from the UK. Thaxter *et al.* (2010) analysed temporal patterns of population change using UK CBC/BBS data for 1967–2006,

showing that the timing of migrant declines appeared to be related to wintering latitude. In general, migrants declining in the period 1967–76 were mainly species wintering in the arid savannahs of the Sahel zone, whereas those declining in the period 1987–2007 tended to be those

wintering further south in the humid tropics (Fig. 1c; see also Van Turnhout *et al.* 2010a).

Long-term systematic ringing studies at European bird observatories and migration stations provide additional, but generally less robust, evidence of A-P declines. Many show declines in long-distance migrants caught (e.g. Hüppop & Hüppop 2010, Berthold & Fiedler 2005) but these results need to be interpreted with caution because ringing totals are not necessarily a reliable measure of trends in bird abundance (Dunn 2002, Hochachka & Fiedler, 2008).

Outside Europe, there are few long-term monitoring studies of A-P migrants. Passage migrants have been trapped at Ngulia, Kenya, every autumn since 1972 (Pearson & Lack 1992) but no recent information has been published on changes in numbers, and variations in the sampling methods over time mean these changes may not reflect population trends. Counts of A-P migrants in Africa are sparse, and the available data are limited even for selected groups of species, such as wetland birds that occur in large aggregations, and highly visible birds of prey. Counts of wintering waterfowl since the 1970s in the major Sahelian wetlands (Senegal and Niger Deltas and Lake Chad) suggest stable or fluctuating numbers of some common migrants (e.g. Garganey *Anas querquedula*, Girard *et al.* 2004, Zwarts *et al.* 2009). However, Ruff *Philomachus pugnax* in the Senegal delta have declined since 1993 (Schricke

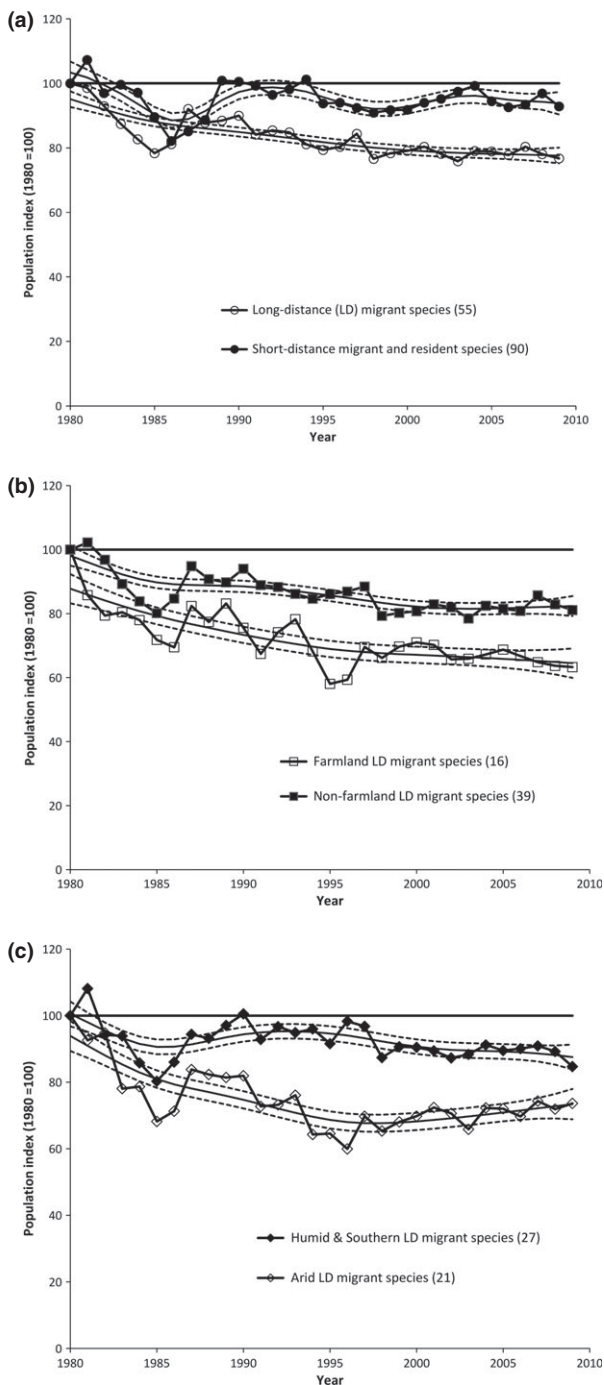


Figure 1. Aggregate multi-species indices for widespread and common European (a) long-distance (LD) migrants (55 species: open circles) and short-distance migrants and resident breeding birds (90 species: closed circles), (b) farmland (16 species: open squares) and non-farmland (39 species: filled squares) long-distance migrants, and (c) long-distance migrants wintering predominantly in the ‘arid zone’ (21 species: open diamonds) and ‘humid & southern zones’ (27 species: closed diamonds) of Africa. Trend data are derived from 25 countries covered by the Pan-European Common Bird Monitoring Scheme (PECBMS). Index values are fixed to 100 in 1980. The non-linear solid lines are statistically smoothed trends derived from the software TRENDSPOTTER, which uses structural time series analysis and the Kalman filter to fit flexible trends (Visser 2004, 2005), and the dashed lines are the 95% confidence limits on the smooth trend. To test for differences between the groups, we calculated the difference between them for each year in the time series and calculated a linear regression through these differences. If this trend deviates significantly from zero, we conclude that the trends are significantly different.

et al. 2001) and roadside counts of raptors in West Africa suggest declines in many migrant species (e.g. Thiollay 2006).

Not all A-P migrants are in decline – some are increasing in number (Table 1, Supporting Information Table S1) and some sub-populations of the same species show contrasting population trends (e.g. Morrison 2011, Morrison *et al.* 2013).

EXTENT OF EVIDENCE FOR POTENTIAL CAUSES OF MIGRANT DECLINES

We attempt to provide a synthesis of factors known to affect individual A-P migrants at different points during the annual cycle by conducting a literature review for each species (see Supporting Information Table S2 for further information on how the review was carried out), and tabulating the existing evidence for effects grouped according to season (breeding and non-breeding), factor (e.g. habitat loss, nest predation) and parameter affected (Table S2).

To identify key knowledge gaps, we examined the extent of published evidence for factors affecting A-P migrants. Assessments of the extent of evidence were derived using information in Table S2, where threats have been demonstrated for individual species, and giving greater weight to impacts with a strong demographic effect. Thus, we categorized the strength of evidence for threats shown to have a population-level effect as ‘strong’, threats affecting survival or breeding success as ‘moderate’, and impacts influencing only habitat selection as ‘weak’. We considered the extent of evidence during the breeding and non-breeding (wintering and staging sites) seasons and for species occupying different breeding and wintering habitats, using the count of species assigned to each class as our measure. Our assessment of the strength of the evidence should not be confused with an evaluation of the size of an effect in the statistical sense. Although such an evaluation would be valuable, it is not possible to establish this in a consistent way across the large number of reported studies.

Figure 2(a) shows the percentage of all A-P migrants allocated to each evidence class, showing that we have a far better understanding of threats to migrants during the breeding season than during the non-breeding season. Information on potential factors was available for 48% of species we assessed

during the breeding season, but only 27% during the non-breeding season, highlighting this knowledge gap. Even the latter figure probably gives an unrealistic impression of the extent of our knowledge because many of these studies correlate estimates of migrant population change or survival derived on the breeding grounds with remotely sensed measures of climate or habitat in Africa, without actually studying the species during the non-breeding season. Note that we might expect a pattern similar to that shown in Figure 2(a) if migrants were impacted to a greater extent by factors during the breeding season than during non-breeding season. However, we consider that this is much more likely to reflect a research bias towards migrants during the breeding season.

Moreover, threats to long-distance migrants during the breeding season are best understood in species associated with farmland and forest (Fig. 2b), which reflects the focus of recent European research on birds in these habitats. Our understanding of factors influencing migratory waterbirds is less complete, although strong and moderate evidence is still available for *c.* 30% of associated species. Threats to birds of tundra/moorland and Mediterranean scrub/forest, occupying habitats at the northern and southern extremes of Europe, are the least well understood. During the non-breeding season, factors influencing migrants are better understood for species associated with arid habitats than those wintering in humid/southern habitats (Fig. 2b). Repeating this assessment for the declining species identified in Table S2 ($n = 61$) produced virtually identical results and does not alter our conclusions.

Considering the evidence for different factors driving population change across all species ($n = 126$, Table 2), our review suggests that human-related habitat change is the most important factor affecting A-P migrants across both the breeding (78%) and the non-breeding grounds (89%). On the breeding grounds, predation and climate change are the next most important factors, followed by several minor ones (e.g. hunting, collision with infrastructure). On the non-breeding grounds, the only factor, in addition to habitat change, with evidence of an impact is hunting (Table 2). Where habitat change is recognized as an important factor on the breeding grounds, most of those studies come from farmland (62%), followed by woodland and scrub habitat (26%), and then wetland (19%). Where habitat change is recognized as such on the

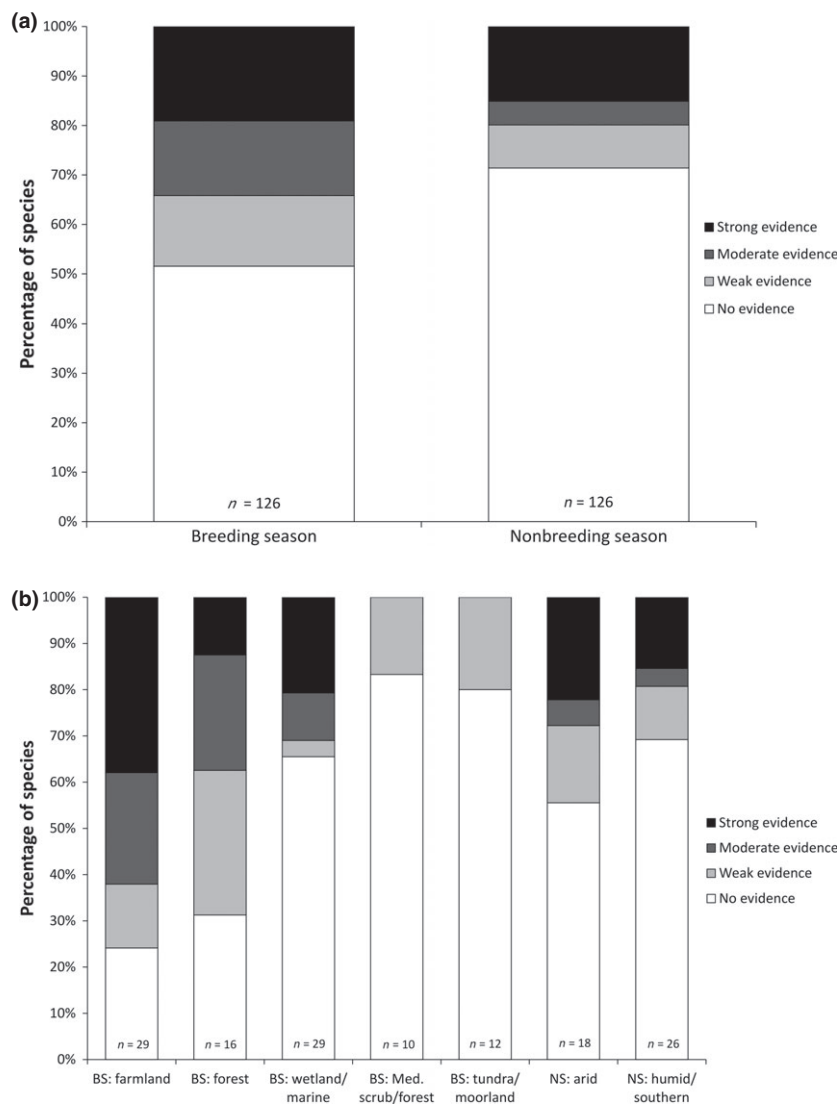


Figure 2. Summary of the extent of evidence supporting an influence of factors on A-P migrants during the breeding and non-breeding seasons. For each migrant, evidence from the published studies catalogued in Table S2 was categorized as either ‘strong’ (a population-level effect), ‘moderate’ (effects on survival or breeding success) or ‘weak’ (an effect on habitat selection), and we counted the number of species assigned to each class. Information is presented separately for (a) all migrants during the breeding and non-breeding seasons, and (b) migrants associated with different breeding and wintering habitats. We based our assessment of non-breeding habitat associations on the scheme outlined in Table S1. Thus, only species for which this assessment is available were included in our analysis; this subset of species comprises a non-random selection of well-studied passerines, and so may not be representative of all species.

non-breeding grounds for A-P migrants, most studies come from wetland (44%), woodland/forest (25%) and savannah/wooded savannah habitats (22%). These figures should not be interpreted as an indication of the relative importance of different factors impacting A-P migrants; factors whose effects are difficult to study will be under-represented in the published literature.

DRIVERS OF CHANGE

Habitat loss/degradation on breeding grounds

In recent decades, significant changes to important breeding habitats in Europe have been implicated in the population declines of many birds, including

Table 2. Extent of published evidence for the impact of different factors and sub-factors (where applicable) on the breeding and non-breeding grounds (wintering and staging) from this review (see Table S2 for full details). The number of species cases (*n*) and percentage (%) of studies demonstrating effects in each category are shown.

Factor	<i>n</i> (%)	Sub-factor	<i>n</i> (%)
(a) Factors affecting A-P migrants on the breeding grounds			
Habitat change	58 (77)	Farmland	36 (62)
		Woodland/scrub	15 (26)
		Wetland	11 (19)
		Riverine	2 (3)
		Marine	2 (3)
Predation	7 (10)		
Climate change	5 (7)		
Collision with infrastructure	2 (3)		
Pollution/pesticides	1 (1)		
Persecution/hunting	2 (3)		
(b) Factors affecting A-P migrants on the non-breeding grounds			
Habitat change	32 (89)	Wetland	14 (44)
		Woodland/forest	8 (25)
		Savannah/wooded savannah	7 (22)
		Farmland	2 (6)
		Other	3 (9)
		Persecution/hunting	4 (1)

A-P migrants. This is particularly true in agricultural areas, but also in woodland and wetland habitats (Table S2). Key changes in agricultural habitats include the homogenization of the agricultural landscape, the intensification of crop management (e.g. changes in fertilizer, pesticide, grazing and cutting/harvesting regimes) and the loss of marginal, natural or semi-natural habitats (e.g. Donald *et al.* 2001, Benton *et al.* 2003, Newton 2004b). The increasing homogeneity of farmland has reduced its suitability as foraging or nesting habitat for several A-P migrants that require a combination of habitat types for breeding or feeding, including the Hoopoe *Upupa epops* (Barbaro *et al.* 2008), Eurasian Wryneck *Jynx torquilla* (Weisshaupt *et al.* 2011), Common Redstart *Phoenicurus phoenicurus* (Schaub *et al.* 2010), Red-backed Shrike *Lanius collurio* (Brambilla *et al.* 2010), Lesser Grey Shrike *Lanius minor* (Wirtitsch *et al.* 2001) and Yellow Wagtail *Motacilla flava* (Gilroy *et al.* 2010).

The intensification of cropped habitats has also impacted several species. For example, the switch

from hay to silage with subsequent earlier and more intensive cutting caused severe adult, nest and chick mortality of Corncrakes *Crex crex* and Whinchat (Green *et al.* 1997, Grübler *et al.* 2008), and intensive cultivation of cereal crops and grasslands may have reduced the breeding success of Yellow Wagtails (Bradbury & Bradter 2004, Gilroy *et al.* 2009).

The loss of marginal, natural or semi-natural habitats may have impacted farmland A-P migrants because they rely on these habitat features for foraging and nesting. For example, Woodchat Shrikes *Lanius senator* require scattered trees in farmland as nest-sites and perches for hunting (Schaub 1996), and the Ortolan Bunting (Menz *et al.* 2009), European Roller *Coracias garrulus* (e.g. Avilés *et al.* 2000) and Red-backed Shrike require hedges or isolated boundary trees as song posts and/or feeding perches (Brambilla *et al.* 2007). Similarly, European Turtle Doves require large mature hedges for nesting close to weed-rich habitats for foraging (Browne & Aebischer 2004). Yellow Wagtails nest in crops in arable landscapes, but forage on emergent insects from water-filled boundary ditches (Bradbury & Bradter 2004, Gilroy *et al.* 2009) and species such as Common Whitethroat forage extensively in invertebrate-rich uncultivated fallows and wildflower areas (e.g. Birrer *et al.* 2007).

Conversely, in other parts of Europe, abandonment of agricultural land has become an issue for some A-P migrant species. In the northwest Mediterranean region, land abandonment was associated with increases in resident/short-distance migrants, largely woodland species, but declines in A-P migrants, such as *Sylvia* warblers favouring open semi-natural habitats (Sirami *et al.* 2007, Fonderflick *et al.* 2010). For some species, such as Red-backed Shrike, intermediate levels of farming intensity offer the optimal habitat composition, with complete abandonment also likely to cause a severe decline in breeding populations (Brambilla *et al.* 2007, 2010).

Böhning-Gaese and Oberrath (2003) showed that long-distance migrants, as a group, favour open breeding habitats (e.g. agricultural land) to a greater extent than residents and short-distance migrants, a preference most likely inherited from savannah-breeding African ancestors. This dependence on open breeding habitats by a larger subset of long-distance migrants may predispose them to being disproportionately affected by changes in European agricultural ecosystems.

Changing patterns of woodland management, such as reduction in traditional coppicing practices, and natural processes of succession and recent increases in deer browsing, have meant that young-growth woodland has been increasingly lost throughout much of Europe, with a shift in woodland age structure towards intermediate-aged stands (e.g. Fuller *et al.* 2007, Hopkins & Kirby 2007). Since many A-P migrants favour early successional habitats to a greater extent than residents (e.g. Helle & Fuller 1988, Fuller & Crick 1992), they may have been particularly sensitive to such changes. In Fennoscandia, intensive forestry has led to the loss of old-growth stands and their replacement with structurally less diverse planted monocultures. The latter may be much less suitable for many bird species, including A-P migrants; they lack a herbaceous understorey required by ground-nesters and may be too dense for aerial-sallying flycatchers (Hausner *et al.* 2003).

The A-P migrants that breed in freshwater wetlands are threatened by direct habitat loss, particularly due to drainage for agricultural reclamation. The globally threatened Aquatic Warbler *Acrocephalus paludicola*, for example, has lost 90% of its favoured sedge fen mire breeding habitat in southwest Belarus since 1960 due to drainage (Kozulin & Flade 1999), and loss of *Phragmites* reed beds from inland wetlands may have contributed to declines in Great Reed Warbler *Acrocephalus arundinaceus* (Graveland 1998). Commercial harvesting of reeds leads to reduced arthropod abundance compared with unmanaged reed beds (Schmidt *et al.* 2005), reducing the suitability for a number of species, including the Eurasian Reed Warbler *Acrocephalus scirpaceus* (Graveland 1999) and Purple Heron *Ardea purpurea* (Barbraud *et al.* 2002). Deterioration in water quality has been shown to impact species such as Black Tern *Chlidonias niger* (e.g. Beintema 1997) and changes in water table management, reduction in standing water and eutrophication have been linked to population trends of resident and migrant marshland birds in The Netherlands (Van Turnhout *et al.* 2010b).

Drought and habitat change in the non-breeding season

Key wintering and staging areas for many A-P migrants in Africa are the wetlands, savannahs and savannah woodlands of the Sahel zone where

ecological conditions are intimately linked to levels of precipitation in the wet season from July to September. If these rains have been good, then food resources will be also be good when migrants arrive. Although rainfall in North Africa has increased since the 1990s (Fontaine *et al.* 2011), drought conditions predominated during the last three decades of the 20th century (Nicholson 2000), almost certainly causing near-irreversible changes in habitats of this region (Zwarts *et al.* 2009). The Sahel drought has been frequently linked to declines of many A-P migrants, including those dependent on both seasonal freshwater and terrestrial habitats in these non-breeding areas (e.g. Peach *et al.* 1991, Zwarts *et al.* 2009).

In wetland habitats, the abundance of Sedge Warblers *Acrocephalus schoenobaenus* and Sand Martins *Riparia riparia* in Britain, for example, varies in relation to rainfall in West Africa. Low rainfall is associated with low annual survival rates and reduced population size in the subsequent breeding season, possibly because drought causes density-dependent overwinter mortality by reducing wetland habitat and hence the carrying capacity of the wintering area (e.g. Peach *et al.* 1991, Norman & Peach 2013). Other A-P migrants (e.g. Purple Heron, Squacco Heron *Ardeola ralloides*, Black-crowned Night Heron *Nycticorax nycticorax*) using seasonal freshwater habitats in West Africa show similar correlations with indices of the wet season (den Held 1981, Zwarts *et al.* 2009).

A-P migrants exploiting terrestrial habitats that have also been shown to be sensitive to climatic fluctuations, particularly drought in their staging or wintering areas, include Common Whitethroats (e.g. Baillie & Peach 1992), White Stork *Ciconia ciconia* (Schaub *et al.* 2005), Barn Swallow *Hirundo rustica* (Robinson *et al.* 2008), Lesser Kestrel (Mihoub *et al.* 2010) and Red-backed Shrike (Pasinelli *et al.* 2011; Table S2). Some studies have noted a close association between African rainfall and invertebrate abundance (e.g. Dingle & Khama 1972, Sinclair 1978). For these terrestrial bird species, the impact of rainfall is probably an indirect one, mediated through change in food availability, but in the absence of field research in key wintering and staging areas, the underlying mechanisms remain unclear. In the Nearctic–Neotropical flyway, a strong positive association has been shown between arthropod biomass and winter warbler abundance (Johnson & Sherry 2001). Furthermore, field studies and experimental

manipulation of winter food availability for Ovenbirds *Seiurus aurocapilla* in wet and dry years has demonstrated a direct relationship between non-breeding season precipitation, food availability and physical condition of the birds (Strong & Sherry 2000, Brown & Sherry 2006).

Poor conditions on the wintering grounds can also carry over to affect arrival dates and reproductive performance on the breeding grounds. Thus, late arrival of Barn Swallows in years when rainfall and primary productivity are low in their southern African wintering grounds may reflect poor body condition and slower moult in dry years, resulting in delayed departure and, ultimately, reduced productivity (Saino *et al.* 2004a,b). Similarly, African rainfall is positively correlated with the migration phenology and the eventual breeding success of White Storks in Germany (Dallinga & Schoenmakers 1987, Bairlein & Henneberg 2000). Once again, evidence for such a carryover effect has been demonstrated in the Nearctic–Neotropical flyway; American Redstarts *Setophaga ruticilla* originating from high-quality tropical winter habitat arrive earlier and have higher reproductive success on the breeding grounds than individuals coming from low-quality winter habitat (Marra *et al.* 1998, Norris *et al.* 2004).

Drought conditions have almost certainly compounded the impact of other human-induced habitat changes in vulnerable zones. For example, Sahelian wetlands have been subject to damming, exploitation for irrigated crops, the conversion of natural floodplain woodlands to plantations of exotic species, changes in grazing regimes, and increased hunting activity. These pressures differ across the major wetlands in the Sahel/Sudan zone (Senegal Delta, Inner Niger Delta, Hadejia-Nguru floodplains, Lake Chad Basin and the Sudd region) and thus impact different bird species and populations at different times in different places (Zwarts *et al.* 2009). Just as these changes are complex, so are the responses of A-P migrants to them. Whereas Ruff and Black-tailed Godwit, which forage in rice crops, apparently benefit from the conversion of floodplains to rice cultivations, Sedge Warblers, which rarely use cultivated rice fields, do not (Zwarts *et al.* 2009).

Wooded savannah dominated by *Acacia* species is a major habitat of the Sahel zone (Morel & Morel 1992) and has undergone widespread deterioration from activities such as clearance for agriculture, wood fuel and grazing exacerbated by

changes in climate and the prevalence of drought (e.g. Wilson & Cresswell 2006, Yiran *et al.* 2012). Information about land cover or land cover change in sub-Saharan West Africa from remote sensing earth observation data is patchy and often at too broad a scale to allow assessment of changes that affect migrant distribution. Where information exists, it suggests extensive loss of forest/woodland habitats. In Senegal, for example, the extent of wooded savannahs and forests is estimated to have declined from 78% of the country's land area in 1965 to 72% in 2000 (a loss of *c.* 33 000 ha per year), with much of the remaining habitat exhibiting moderate to severe degradation from charcoal production (Tappan *et al.* 2000, 2004). Severe deforestation of Sahelian wooded savannah has also been documented at smaller spatial scales in Senegal (Morel & Betlem 1992, Gonzalez 2001), northeastern Nigeria (Geomatics 1998, Cresswell *et al.* 2007), northern Ghana (Yiran *et al.* 2012) and northeastern Somalia (Oduori *et al.* 2011). The same may be true for Mali, Niger, Burkina Faso and Sudan (Grimmett 1987), and this forest loss and degradation is predicted to continue throughout much of sub-Saharan West Africa (Gaiser *et al.* 2011, Heubes *et al.* 2011).

Forest loss and degradation is likely to have a significant negative impact on populations of A-P migrants dependent on them (e.g. Jones 1985, Morel & Morel 1992, Jones *et al.* 1996, Wilson & Cresswell 2006), although documented responses to habitat change differ between species. Deforestation has been shown to result in decreases in Common Whitethroat and Subalpine Warbler *Sylvia cantillans* but in increases in Western Bonelli's Warbler *Phylloscopus bonelli*, Yellow Wagtail (Cresswell *et al.* 2007), Northern Wheatear (Wilson & Cresswell 2010) and Whinchat (Hulme & Cresswell 2012). Dry season farmland, much of which was open savannah woodland in West Africa, can support good numbers of open country species, such as Whinchat and Wheatear. It has been suggested that Whinchats may even benefit from anthropogenic change on their wintering grounds (Hulme & Cresswell 2012) in the same ways that some agricultural habitats, specifically tree crops such as *Citrus* spp. and shaded coffee *Coffea* sp., can be valuable for Nearctic–Neotropical migrants (e.g. American Redstart, Johnson *et al.* 2006).

Habitat degradation in the Sahel zone may also have impacts on a suite of species for which this is a refuelling stage before or after crossing the Sahara

desert. In the absence of field studies in sub-Saharan West Africa, knowledge on where species fatten and the ecological strategies they adopt remains poor. Recent studies suggest A-P migrants may need less fat reserves to cross the Sahara than previously thought (Salewski *et al.* 2010a,b) and have considerable flexibility in fattening strategy (Dierschke *et al.* 2005, Delingat *et al.* 2006), but the balance of evidence still supports the view that spring and autumn passages over the Sahara are periods of extremely high energy demand for many species (Newton 2006, 2008). The refuelling strategies that different species employ on migration (e.g. Bairlein 1985, Schaub & Jenni 2000, Arizaga *et al.* 2013) will influence the extent to which conditions in the Sahel affect their survival. Some apparently increase their fuel accumulation closer to the border of the Sahara, with the most important pre-migratory fattening sites in spring around the southern edge of the Sahel (e.g. Ottosson *et al.* 2002, Salewski *et al.* 2002). Other species may fatten gradually much further south, e.g. Garden Warbler *Sylvia borin*, Pied Flycatcher and Yellow Wagtail, making them less dependent on a small number of high-quality stopover sites in the Sahel (e.g. Bell 1996, Salewski *et al.* 2002, Ottosson *et al.* 2005, Bayly & Rumsey 2010, Jenni-Eiermann *et al.* 2011).

Similarly, during the southern migration, some species migrating from Portugal to Senegal refuel en route (e.g. Common Grasshopper Warbler *Locustella naevia*, Bayly *et al.* 2011), some accumulate fat deposits at staging sites adjacent to the boundary of the Sahara (e.g. Eurasian Reed Warbler and Common Whitethroat, Schaub & Jenni 2000; Garden Warbler, Bairlein 1991), and others do not accumulate appreciable fat deposits at all during their migration and may rely on foraging opportunities within the Sahara itself (e.g. Spotted Flycatcher, Schaub & Jenni 2000).

For some species on northward spring migration, the fruits of shrubs, such as *Salvadora persica*, are a major dietary component during pre-migratory fattening (Jones 1985, Stoate & Moreby 1995). If fruit and berry abundance in the Sahel are reduced by habitat degradation, this may be reflected in reduced body condition (e.g. Common Whitethroat, Stoate 1995) or may force individuals to refuel earlier and further south, effectively increasing the Sahara crossing distance and so perhaps also the energetic cost (Ottosson *et al.* 2002, Wilson & Cresswell 2006).

To date, the great majority of studies have highlighted drought and habitat degradation in the Sahel as a key issue. However, the recently suggested declines of A-P migrants wintering in the Guinea forest-savannah and Guinea moist forest zones of Africa (Hewson & Noble 2009, Thaxter *et al.* 2010) indicate that other factors may now also be operating. Although these species pass through and may refuel in the Sahel, their more recent pattern of decline suggests that factors in the more southern zones may have become increasingly important. Forests in these more southerly zones have also declined in extent, and possibly in quality, for migrant birds (Brink & Eva 2008, Yiran *et al.* 2012). Agricultural expansion is the most significant cause of deforestation. Remotely sensed land cover data for sub-Saharan Africa suggests a 57% increase in agriculture between 1975 and 2000 at the expense of natural vegetation, a loss of almost 5 million hectares of forest and non-forest natural vegetation per year (Brink & Eva 2008). In countries such as Cote D'Ivoire, Ghana and Nigeria, 83% of what were once dense forests are now forest-agricultural mosaics and the production of the major food crops, such as cassava and plantain, has increased markedly in the humid lowlands (Norris *et al.* 2010).

Finally, the quality of important staging areas in northern Africa and Europe may also be declining for migrants. For example, refuelling rates of Ruff in grasslands in The Netherlands, the western major staging site, have declined as it has become intensively managed for dairy production. This has been reflected in a global redistribution of breeding Ruffs, with a decline in the western flyway population breeding in Europe and the European Arctic, and an increase in the eastern one, staging in Belarus and breeding in Western and Central Siberia (Verkuil *et al.* 2012). Similarly A-P migrants staging in southern Morocco during spring northbound migration ultimately rely on good feeding conditions for continuing migration (Maggini & Bairlein 2011, Arizaga *et al.* 2013).

Effects of climate change on breeding and non-breeding grounds

Bioclimatic models predict a shift in the geographical ranges of A-P migrants, suggesting that their potential future breeding ranges (under climate scenarios for 2070–2099) in Europe might be on average only 89% of their present range, and

potential future and present distributions might only overlap by 42% (Huntley *et al.* 2008). Other studies have suggested that trans-Saharan passerine migrants may suffer winter range reductions in the future, but the current range data for Africa on which these studies are based are generally poor (Barbet-Massin *et al.* 2009). A study of *Sylvia* warblers demonstrated that, whereas potential breeding ranges were anticipated to move northwards, potential non-breeding ranges showed no consistent directional shift. Importantly, however, migration distances, and thus energetic costs, between breeding and wintering grounds were projected to increase (Doswald *et al.* 2009), although in practice a few species have shown the opposite trend (e.g. Barn Swallow, Ambrosini *et al.* 2011).

Climatic change may also disrupt the synchrony of bird–prey dynamics. Migrants may be particularly vulnerable to phenological mismatch (Both & Visser 2001, Both *et al.* 2006) because their arrival dates on European breeding sites may be constrained by conditions in non-breeding areas, and there are likely to be fitness consequences of arriving too early or too late. Many studies of spring migration phenology report a greater advancement in short-than long-distance migrants (e.g. Rubolini *et al.* 2007, Saino *et al.* 2011), a trend that could cause differences in susceptibility to mismatch (Knudsen *et al.* 2011). However, some studies have found no difference (Hüppop & Hüppop 2003, Zalakevicius *et al.* 2006), or even the reverse pattern (Stervander *et al.* 2005, Jonzén *et al.* 2006). These inconsistencies may be real or a result of using different methods (Lehikoinen & Sparks 2010), or even sampling effects whereby smaller population sizes lead to apparent later arrival.

The key question, however, is whether these observed shifts in migration and breeding phenology have been sufficient to track changes in resource peaks in breeding areas, usually food, although for Common Cuckoo, host nests may also be important (Møller *et al.* 2011, but see Douglas *et al.* 2010). Studies of Pied Flycatchers breeding in The Netherlands (Both & Visser 2001, Both *et al.* 2006) showed that populations have advanced the onset of egg-laying by as much as 10 days over two decades, but some populations no longer lay synchronously with the window of peak food availability (Both & Visser 2001), with populations nesting late relative to food peaks declining more than those nesting relatively early.

Pied Flycatchers may use endogenous responses to environmental cues (e.g. photoperiod) to initiate spring migration in Africa and because these cues do not necessarily reflect conditions on the breeding grounds, this may constrain their capacity to respond adaptively to climate change. Alternatively, it may also be that different climatic trends in breeding and passage areas act as a climatic barrier, similarly disrupting synchrony between timing of breeding and peak food availability (Hüppop & Winkel 2006).

Insectivorous A-P migrant species in The Netherlands declined strongly in forests, a habitat characterized by a short spring food peak, whereas those living in marshes with less seasonal food peaks have declined less. Within these forests, species arriving later in spring declined most, probably because mismatch with the peak food supply was greatest (Both *et al.* 2010). Furthermore, A-P migrants in forests have declined more severely in Western Europe, where springs have become markedly warmer, compared with northern Europe, where temperatures during spring arrival and breeding have increased less (Both *et al.* 2010). Mismatch has also been suggested as one of the possible causes of the relationship between timing of migrant declines in the UK and wintering latitude, with species wintering further south tending to exhibit more recent declines (Thaxter *et al.* 2010, Ockendon *et al.* 2012).

Overall, however, few studies explicitly address the effects of trophic mismatches on A-P migrants, and the generality of its link to population declines has not been established (Knudsen *et al.* 2011). For example, in The Netherlands, Pied Flycatcher populations are showing clear evidence of trophic mismatch, whereas further east in Germany they are doing well, and even show evidence of a climate-related increase in productivity (Winkel & Hudde 1997). The advancement of the timing of caterpillar peaks appears to have had no measurable effect on nestling development, productivity or population trends of Wood Warblers in the UK and Poland (Mariarz & Wesolowski 2010, Mallord *et al.* 2012). Furthermore, broader evidence suggests that A-P migrant population trends are more strongly correlated with migration distance than with phenological mismatch of temperature trends in the breeding and wintering area, although migration distance and phenological mismatch may be linked (Jones & Cresswell 2009, Knudsen *et al.* 2011).

A slightly different form of phenological mismatch has been suggested to occur in the long-distant migrant Common Cuckoo *Cuculus canorus*. Although it parasitizes other long-distant migrants, resident and short-distance migrant birds are also hosts and if these advance their lay dates, with increasing spring temperatures, their phenology may be increasingly poorly matched with that of the Cuckoo (Møller *et al.* 2011). However, support for changes in host availability as a major driver of Cuckoo declines is mixed (Douglas *et al.* 2010).

Changes in weather conditions on passage may also affect arrival dates and breeding phenologies (Newton 2010). For example, the median arrival date of a Finnish population of Pied Flycatcher was negatively associated with temperatures in northern Germany, an important passage area. However, although the birds arrived early in response to increasing temperatures in northern Germany, they did not initiate breeding attempts any earlier, probably because temperatures on the breeding ground remained consistent during the study period (Ahola *et al.* 2004). In years of high productivity in passage sites in the western Mediterranean (indicating higher vegetation production and possibly therefore higher arthropod prey availability), trans-Saharan migrants tended to delay departure. This may be because they trade off early arrival with the certainty of accumulating sufficient energy reserves, or because good conditions allow more poor quality individuals to survive and these tend to have later migration (Robson & Barriocanal 2011).

Climatic change for migrants may also disrupt competitive relationships between resident and migrant bird assemblages or create completely new species interactions (Böhning-Gaese & Bauer 1996, Wiens *et al.* 2009). It has been suggested that migrants are inferior competitors compared with resident species, and that they are excluded from habitats in which residents occur at high densities (Herrera 1978). It is also possible that higher winter temperatures associated with climate change might improve the overwinter survival of resident species, increasing their numbers in the breeding season and hence the severity of inter-specific competition with migrants. Although, in a limited number of sites, the fraction of the bird community consisting of migrants can be predicted from observed changes in climatic parameters (Lemoine & Böhning-Gaese 2003, Lemoine *et al.* 2007),

there is little empirical evidence demonstrating such antagonistic competition between residents and migrants in Europe. Furthermore, species interactions may vary in relation to the density of potential competitors and switch from positive to negative along environmental gradients (Mönkkönen *et al.* 2004) such that interactions may, in some cases, be positive (Mönkkönen & Forsman 2005).

Hunting on passage and non-breeding grounds

A-P migrants are widely hunted (shot and trapped) during both spring and autumn passage through the Mediterranean region (e.g. Magnin 1991, McCulloch *et al.* 1992, Stronach *et al.* 2002). This is particularly evident in areas of southern France, northern Iberia, Italy, Greece, and Turkey, the islands of Cyprus and Malta, and the Maghreb region of northwest Africa (McCulloch *et al.* 1992), where large numbers have been reported killed in the past (Magnin 1991). Studies of individual quarry species suggest large numbers may be hunted annually: for example, 116 000 and 205 000 Common Quail *Coturnix coturnix* in two consecutive autumns (1989 and 1990) in the North Sinai, Egypt (Baha el Din & Salama 1991), and 2–4 million European Turtle Doves across a number of EU countries, a sizeable fraction of the estimated total European population (3.5–7.2 million pairs, BirdLife International 2004, Boutin 2001).

Some species are also hunted on the non-breeding grounds, although the capture and killing of large numbers of birds for consumption in sub-Saharan Africa is relatively restricted to certain species and locations, e.g. terns caught in considerable numbers in coastal West Africa (Everett *et al.* 1987, Grimmett 1987), and large numbers of White Storks hunted in the Sudan (Grimmett 1987) and Mali (Thauront & Duquet 1991). It has also been suggested that the cause of reduced survival of migrant wildfowl, such as Garganey, in years with little flooding is due to increased hunting pressure as birds become concentrated in a few accessible localities (Zwarts *et al.* 2009). In the Inner Niger Delta, a hotspot of such activity, the annual catch of Garganey has been estimated as 1800–27 000 birds, an annual loss of 1–15% of the western wintering population (Senegal–Mali) and 20 000–80 000 Ruff, 15–60% of the population wintering there. Catches

are higher in dry years when birds concentrate in remaining wetlands and the impact of hunting on survival is difficult to distinguish from that of drought (Zwarts *et al.* 2009).

The extent of flooding in large deltas such as the Inner Niger has declined in recent years as dams are constructed and water extracted, particularly for crop irrigation. This further concentration of birds in remaining wetlands alongside increased human population pressure may have increased hunting mortality (E. Wymenga pers. comm.). In addition to those species for which there are estimates of numbers, species such as Barn Swallow, European Turtle Dove, European Honey-buzzard *Pernis apivorus* and Yellow Wagtail are also regularly hunted on their African wintering grounds (Grimmett 1987).

Few studies have shown population-level impacts of this considerable hunting pressure, largely because the relevant data do not exist (e.g. McCulloch *et al.* 1992), and hence the impact is almost impossible to quantify. Although hunting mortality in autumn may in theory be compensated for by density-dependent reduction in winter mortality, there is far less scope for such compensation for spring hunting mortality. For some key, declining, quarry species, such as Turtle Dove, analyses of survey and demographic data from European breeding grounds may be valuable in establishing the extent to which reduced overwinter survival, perhaps linked to hunting mortality, is a key driver of the decline. However, although the effects of hunting on some species may well be considerable, particularly in the eastern Mediterranean, it is probably not an important driver of declines for a large number of A-P migrants.

Other factors – predation, collision with infrastructure and pesticide use

Nest predation has been implicated in the decline of Neotropical migrants and it has been suggested that, because A-P migrants lay fewer clutches than closely related sedentary congeners, they may be particularly vulnerable to nest predation (e.g. Bruderer & Salewski 2008). However, there are few convincing examples of this, except perhaps the Black-tailed Godwit, although here increased numbers of predators have occurred simultaneously with agriculture-related habitat changes that may have reduced cover and food availability (Schekkerman *et al.* 2009).

Particularly during the period of migration, collision with human infrastructure (e.g. wind turbines, television masts, electricity pylons, lighthouses) can sometimes be a source of substantial mortality (Newton 2006). The increasing number of wind turbines is a cause for concern and may be an increasing risk for migrating raptors throughout the flyway. However, demonstrating population impacts of collisions with such infrastructure is difficult. There is some evidence that mortality of adult Egyptian Vultures, as a result of collision with wind turbines, may have contributed to declines in European breeding numbers (Carrete *et al.* 2009), and power line collision accounts for as much as 25% of the White Stork juvenile mortality in Switzerland (Schaub & Pradel 2004).

Finally, pesticide use has long been suggested as a possible driver of declines of A-P migrants (Berthold 1973, Mullie & Keith 1993), particularly the large quantities used over vast areas to control populations of orthopterans, e.g. plagues of Desert Locust *Schistocerca gregaria* (Dallinga & Schoenmakers 1987, Newton 2004a, Sanchez-Zapata *et al.* 2007). These impacts are likely to be indirect, e.g. reducing abundance of important prey, rather than resulting in direct mortality, but to date no studies have linked pesticide use to population-level effects (although see White Stork below). In one study, the abundance of Afrotropical birds (not A-P migrants specifically) on plots treated with pesticides (aerial spraying of locust-control pesticides) declined significantly compared with control plots over a period of 3 months (Mullie & Keith 1993), but only a fraction of the observed bird mortality (*c.* 7%) on the plots could be attributed to direct contamination. The implementation of locust-control measures in Sahelian Africa has been associated with a decline in both the occurrence and the extent of plague events (Rainey *et al.* 1979, Van Huis *et al.* 2007). For the White Stork, abundance in Central Europe is higher following winters with high numbers of locusts, compared with summers following poor locust years (Dallinga & Schoenmakers 1987), and it is conceivable that reduced food (locust) availability in Africa may have contributed to the declines of other large trans-Saharan migrants. However, Moreau (1972) suggested that locust peaks are sporadic and irregular, and in the intervening period there is a greater dependency on local solitary orthoptera (e.g. Montagu's Harrier, Trierweiler *et al.* 2013). Nevertheless, it is also

possible that the disruption of natural cycles of the Desert Locust may have cascading effects in the Sahelian ecosystem, causing disruption over several subsequent years (Sanchez-Zapata *et al.* 2007).

KEY GAPS IN KNOWLEDGE AND FUTURE RESEARCH DIRECTIONS

Our synthesis of information relating to A-P migrants reveals that knowledge gaps exist for a broad cross-section of species and for factors operating in both the breeding and the non-breeding season (Table 2 and Fig. 3). Although it is tempting to attribute the causes of declines to a few factors, there are likely to be different factors operating on individual species and even sub-populations of the same species and it is likely that these will have changed over time and may continue to do so. However, we can identify several priority areas for research which will greatly assist the diagnosis of the causes and result in the greatest progress:

- the use of new and emerging tracking technologies,
- detailed field studies of migrant birds in sub-Saharan west Africa,
- better use of survey and demographic data from the European breeding grounds, and
- use of remote sensing earth observation data of land cover change in sub-Saharan west Africa.

The use of new and emerging tracking technologies

Until recently, tracking small animals has relied on indirect methods such as stable isotopes (e.g. Hobson *et al.* 2004, Oppel *et al.* 2011), which provide useful insights but are geographically imprecise (Bächler *et al.* 2010). Among direct tracking methods, satellite telemetry has been a key advance in the study of large-bodied birds, particularly migrating raptors and storks (e.g. White Stork, Berthold *et al.* 2001; Osprey *Pandion haliaetus*, Hake *et al.* 2001; Montagu's Harrier, Trierweiler *et al.* 2007). Moreover, GPS and GSM tracking technologies are becoming more advanced (for reviews see Bridge *et al.* 2011, Guilford *et al.* 2011), allowing location accuracies of a few metres.

The current size and weight of satellite and GPS tags renders them still unsuitable for many species (Bridge *et al.* 2011) but the development of light-level geolocators is proving a new and

powerful tool for studying migratory movements of small birds. Although there are shortfalls of and complications with the accuracy and/or calibration of geolocators, within the African–Eurasian flyway they have already been used to identify wintering and staging areas of several species (e.g. Hoopoe, Bächler *et al.* 2010; Lesser Kestrel, Catry *et al.* 2011; Common Swift *Apus apus*, Åkesson *et al.* 2012; Northern Wheatear, Bairlein *et al.* 2012; Whinchat, Kristensen *et al.* 2013). Crucially, they also provide a means to study the extent of migratory connectivity (e.g. Hoopoe, Bächler *et al.* 2010, Cormier *et al.* 2013) and, when combined with remotely sensed land cover data, can also be used to examine habitat use (Fraser *et al.* 2012, Trierweiler *et al.* 2013). They have revealed the extent to which routes vary between individuals (Bächler *et al.* 2010, Catry *et al.* 2011), the use of more limited geographical areas during migration than expected (Åkesson *et al.* 2012), and that birds can travel much further (e.g. Egevang *et al.* 2010, Bairlein *et al.* 2012), faster (Klaassen *et al.* 2011) or slower than previously thought (e.g. Tøttrup *et al.* 2011, 2012). However, currently even the smallest light-level geolocators are still too heavy for the smallest migrants.

A clear research priority is to maximize the use of these new emerging tracking technologies to identify migratory pathways and strategies. The increase in capabilities of miniature tracking devices such as geolocators and satellite tags is revolutionizing migration studies. The continued reduction in weight of such devices means that before long, tracking studies will be feasible even for the lightest A-P migrants. Such studies will enable the identification of key wintering and staging areas, the analysis of conditions at such areas in relation to migration phenology (e.g. Tøttrup *et al.* 2012), an assessment of the link between breeding and wintering populations, the identification of cross-seasonal interactions, and the detection of relationships between key demographic drivers of population change and environmental factors at the appropriate geographical scales. The understanding of migratory connectivity (i.e. the pattern of linkage between the breeding and non-breeding grounds and staging areas of particular A-P migrant populations) is crucial for effective conservation, as has been well demonstrated in the Nearctic–Neotropical flyway (e.g. Martin *et al.* 2007, Stutchbury *et al.* 2009). In addition, tracking studies will allow field research to be targeted

more effectively; a lack of basic knowledge of staging and wintering areas is a major barrier to understanding population declines, but tagging alone is not enough.

Field studies of migrant birds in sub-Saharan west Africa

A second research priority is to undertake detailed field studies of A-P migrants in sub-Saharan Africa and in staging areas. We know remarkably little about the ecology of even common A-P migrants once they leave Europe. We often lack basic information on aspects of their non-breeding ecology, including distributions, within-season movements, habitat use and foraging ecology. To date, most evidence for drivers on the wintering grounds is indirect, derived largely from correlations between changes in breeding populations and demographic rates and rainfall in West Africa (Winstanley *et al.* 1974, Peach *et al.* 1991). Identifying the mechanistic links between occupancy of different habitat types by migrants and the impact of changes in rainfall and land use in winter and during staging and population change requires intensive field research in the wintering and staging areas (e.g. Maggini & Bairlein 2011, Arizaga *et al.* 2013, Trierweiler *et al.* 2013). Since recent declines have been more marked in species wintering in more southern humid forest zones, we suggest fieldwork here should be a priority. Such studies greatly enhanced the understanding of declines of Neotropical–Nearctic migrants (e.g. Johnson & Sherry 2001, Norris *et al.* 2004, Brown & Sherry 2006).

Better use of survey and demographic data from the European breeding grounds

A third priority should be to make better use of the wealth of survey and demographic data from the European breeding grounds. Some of the seminal work on declining A-P migrants involved the use of ringing and breeding survey data from northwest Europe to pinpoint reduced overwinter survival, linked to Sahel droughts, as a key driver of the declines (Winstanley *et al.* 1974, Peach *et al.* 1991, Bairlein & Henneberg 2000). Every opportunity should be taken to develop collaborative analyses to explore the potential of these data to investigate the spatial and temporal patterns of demographic parameters, and to relate these to migratory

pathways and large-scale patterns of habitat change and climatic factors. Many countries in Europe already have well-developed schemes for monitoring bird populations (e.g. <http://www.ebcc.info/pecbm.html>) and demographic rates (e.g. <http://www.euring.org/>). A priority should be to expand the spatial coverage of such programmes, particularly in Central and Eastern Europe, and foster integrated analyses across European countries.

Use of remote sensing earth observation data of land cover change in sub-Saharan west Africa

The fourth priority is to make better use of remote sensing earth observation data to improve our understanding of how and where land cover is changing across these extensive areas of sub-Saharan West Africa and, crucially, how this relates to A-P migrants. Broad assessments of land cover or land cover change exist for only parts of the region (e.g. Tappan *et al.* 2004). Knowledge of the habitat requirements of migrants will inform the types of land cover that need to be accurately separated by the interrogation of satellite images. Landsat images (30-m spatial resolution) are an ideal starting point for such assessments. However, differences in land cover relating to the habitats that affect migrant distribution may only be resolvable from very high-resolution and hyperspectral sensors that have only become available in recent years, and thus the baseline for change analysis postdates the onset of migrant declines. However, establishing a baseline with which future assessments can be compared should be a priority. In addition, we also suggest that comparing broad spatial patterns in phenology with population data could quantify the extent to which changes in vegetation on non-breeding areas might be affecting breeding populations and help to direct future research.

There are clearly other valuable avenues of investigation, such as increasing information about Eastern, rather than Western European populations, about breeding ecology of woodland, rather than farmland species, and about the impact of hunting for key quarry species. However, our review suggests the greatest progress will be made by studies in the four areas above. The results of this work need to inform a flyway approach to conservation that does not examine drivers or migration phases in isolation, but attempts to

evaluate a suite of drivers across the migratory cycle. This approach has been used by researchers investigating Neotropical migrant birds to great effect (e.g. for American Redstart *Setophaga ruticilla*, Marra *et al.* 1998, Norris *et al.* 2004). It will require extensive collaboration across continents (e.g. Bairlein 1998, 2004) as well as the use of a diverse range of research tools, including use of emerging technology in tracking devices, detailed autecological studies, long-term datasets for birds, and land use and climatic data at national and international scales.

Finally, although beyond the scope of this review, implementing solutions for the conservation of A-P migrants will also require a socio-economic dialogue. Many of these migrants, particularly passerines, occur in relatively low densities over a large geographical area, a situation that lends itself to landscape measures rather than a protected areas approach to conservation. Many of the people inhabiting these landscapes depend on the resources the land provides, particularly through the cultivation of crops and grazing. Research will be necessary to understand how to influence land management practices, including aspects such as understanding the scale at which land management decisions are made and the key stakeholders influencing those decisions. Combining biological and socio-economic data is vital to improve our understanding of land management practices that integrate the needs of birds (and other biodiversity) and people in these areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. To explore the population trends of selected European Afro-Palearctic migrants covered by the Pan-European Common Bird Monitoring Scheme (PECBMS), we have divided the 55 long-distance migrants into those breeding on farmland and non-farmland, and into those characteristic of arid or humid and southern wintering grounds.

Table S2. Summary of our understanding of factors impacting Afro-Palearctic migrants on their breeding, non-breeding and staging grounds.