Migration, Patchiness, and Population Processes Illustrated by Two Migrant Pests

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*New technologies are improving scientists' understanding of the links between sources and destinations of subpopulations of migrants within populations as a whole (metapopulations). Such links and the importance of environmental patchiness are illustrated by migrations of two major pests, the red-billed quelea (*Quelea quelea*) and the desert locust (*Schistocerca gregaria*). The spatiotemporal distribution of rainfall determines where and when* Quelea *can breed, as shown for* Quelea *populations in southern Africa. Numbers and distributions of swarms of desert locusts in four different regions of their huge invasion area (29,000,000 km^2) were analyzed as local populations of a metapopulation. Lagged cross-correlations of seasonally adjusted monthly data demonstrate links between the local populations, which vary in significance according to the pairings of regions analyzed and the lengths of the lags, illustrating the strength of the connectivity between them. Understanding such relationships is essential for predictions concerning future climate change scenarios.*

Keywords: connectivity, rainfall, wind, desert locust, red-billed quelea

In this article we consider how migration, environment, and population processes interact within the "migration system" outlined by Dingle and Drake (2007). This system is an elaboration of the proposition by Drake and colleagues (1995) of a conceptual migration model incorporating aspects of (a) the environment in which migration occurs (the "migration arena"), (b) the spatiotemporal population demography that results from migration (the "population trajectory"), (c) the traits that implement migration and determine the fitness of the migrants (the "migration syndrome"), and (d) the genetic complex underlying the migration syndrome.

We concentrate on the migration arena and population trajectory when discussing the migration systems of terrestrial birds and insects and how some of these organisms' movements interact with environmental variability. In doing so, we briefly describe some novel approaches (connectivity, carry-over effects, and metapopulations) and techniques (satellite telemetry, stable isotopes, and molecular methods) that are being used to improve understanding of migration. Much of such current research is focused on the Americas or on Palaearctic–Afrotropical migrants in their European breeding quarters. To help redress this imbalance, we highlight work on the movements of two migrant species: the red-billed quelea (*Quelea quelea*), which is a major agricultural pest in sub-Saharan Africa, and the desert locust (*Schistocerca gregaria*), which devastates crops in Africa, the Middle East, and Asia. *Q. quelea* and *S. gregaria* have yet to be studied using satellite telemetry, and little is known about carry-over effects among them; nonetheless, we can illustrate recent advances in understanding their migrations by using a metapopulation approach to study their movements and by presenting the results of molecular and connectivity analyses.

Insect migrations differ from bird migrations in that insects seldom perform seasonal circuit migrations in the way that, for example, barn swallows (*Hirundo rustica*) do. These birds, and many other Palaearctic migrants, breed in Europe and spend their winters in Africa, returning to the same locations in each continent year after year. This migratory pattern is not typical of insects, but some insects, such as the monarch butterfly (*Danaus plexippus* L.), do perform a form of seasonal circuit migration, although more than one generation may be involved in a round trip (Dingle et al. 2005, as modeled by Yakubu et al. 2004). Blackflies such as savanna cytospecies of the *Simulium damnosum* species complex, which are vectors of onchocerciasis, or "river blindness," migrate up to 500 km. They travel north with the advancing rain fronts of

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the Intertropical Convergence Zone (ITCZ) in West Africa, to breed in rivers that flow only in the wet season (Garms et al. 1979, Cheke and Garms 1983, Baker et al. 1990). Later, their descendents return south to repopulate perennial rivers during the dry season.

The ITCZ also determines the migrations of birds within Africa, where a variety of movement patterns is known. These patterns were summarized for Nigeria by Elgood and colleagues (1973), who recognized three main categories of intra-African migratory birds. The first category consists of transequatorial migrants such as the pennant-winged nightjar (*Macrodipteryx vexillarius*), which breeds in the southern tropics and winters north of the equator, and Abdim's stork (*Ciconia abdimii*), which winters in southern Africa but breeds in the Sahel during the rains. The second category includes migrants within the northern tropics with exclusive breeding and nonbreeding geographical ranges. For instance, the grey-headed kingfisher (*Halcyon leucocephala*) follows the same pattern as the blackflies, moving north with the rains in April and May, and retreating southward in October to breed in the winter. However, there are also birds such as the white-throated bee-eater (*Merops albicollis*) that do the opposite of the blackflies, moving south with the rains and returning north to breed in the dry season. The third category consists of species with overlapping breeding and nonbreeding ranges that concentrate in the south in the dry season (e.g., the variable sunbird [*Cinnyris venustus*]) and of species that concentrate in the north in the dry season (e.g., the cattle egret [*Bubulcus ibis*]). These examples from West African birds are just a few of the many and varied migration patterns known among animals, and differences between patterns are attributable to dietary and nesting requirements, population pressures, and environmental determinants. Synopses of migration systems in other continents have been provided for the Americas by Jahn and colleagues (2004), for Asia by Irwin and Irwin (2005), and for Australia by Griffioen and Clarke (2002). To reveal how this extensive variation in migration strategies has evolved, we need research linking the population dynamics and genetic compositions of subpopulations with data on the breeding success of individuals adopting different migratory strategies.

In some bird species (e.g., the starling [*Sturnus vulgaris*] and blackbird [*Turdus merula*]) and insects (e.g., the brown planthopper [*Nilaparvata lugens*]), some individuals migrate and others do not (e.g., in *N. lugens,* long-winged forms move but brachypterous morphs do not), a phenomenon often under density-dependent control. This "partial migration" (Lack 1943, 1968) is reported in 70% of South American migrant bird species (Stotz et al. 1996, Jahn et al. 2004) and in 60% of migrant bird species from Europe (Berthold 2001), while various degrees of "nomadism" are frequent in desert species (Dean 2004). Migrations vary enormously in terms of their spatial topologies and scales, periodicities, and timing, each of which can influence population processes.

Table 1 summarizes spatiotemporal movements by birds in terms of their scale, varying from local movements to seasonal circuit migrations such as those of the barn swallow. Analyses of the proportions of all species of British and Irish birds, of different ages and sexes, that migrate, and many other aspects of the migration system, have been provided by Wernham and colleagues (2002). Such summaries emphasize how varied migration patterns are and how difficult it is to generalize about them. In this article we illustrate how new techniques and new concepts are helping to elucidate the forces affecting migration patterns, not least the role of environmental variation.

Environmental conditions are paramount in controlling migration and population processes at various scales (Sæther et al. 2006). Evidence is mounting that migration patterns are altering with current changes in climate, and this has already been shown by phenological shifts (Cotton 2003, Jenni and Kéry 2003), such as the earlier spring migrations by *Tringa* sandpipers (Anthes 2004). Climatic conditions have been determinants of the evolution of many migration systems, and

Table 1. Examples of movements and migration by birds according to time and space.

		Space	
Time	**Short (< 50 km)**	**Medium (50–100 km)**	**Long (> 100 km)**
Daily	Foraging from roosts or nests to feeding or drinking stations (e.g., *Quelea quelea;* Ward 1978, Elliott and Allan 1989)	Flights to waterholes by Namaqua sandgrouse (*Pterocles namaqua;* Urban et al. 1986)	Foraging by seabirds (Weimerskirch et al. 2002)
Intra-annual	Altitudinal movements (e.g., Gurney's sugarbirds [*Promerops gurneyi*] move 6–10 km downhill in search of nectar from *Protea* and other flowers [De Swardt 1991]; ptarmigan [*Lagopus mutus*] and grey wagtails [*Motacilla cinerea*] move to and from upland areas [Mead 1983])	Cold-weather movements (e.g., skylarks [*Alauda arvensis*]); seasonal movements, both altitudinal and nomadic, in search of flowering plants by sunbirds (*Nectarinia* spp.) and *Drepanorhynchus reichenowi* (Craig and Hulley 1994, Cheke and Mann 2001)	Cold-weather movements (e.g., wildfowl and waders within wintering range; Wernham et al. 2002)
Annual	Movement of tits (*Parus* spp.) from woodland breeding habitat to suburban gardens (Perrins 1979)	Altitudinal movements (e.g., golden plover [*Pluvialis apricaria*], twite [*Carduelis flavirostris*]) from high breeding grounds to lower levels in winter (Wernham et al. 2002)	Intracontinental movements (e.g., *Quelea quelea* [Ward 1971], redwings [*Turdus iliacus*] within Europe [Roberts and White 2006]); intercontinental movements (e.g., Palaearctic birds to and from Africa)
Irregular	Ranging, local nomadism (e.g., brown-necked raven [*Corvus ruficollis*] and Asian desert sparrow [*Passer zarudnyi*]; Dean 2004)	Nomadism (e.g., spotted sandgrouse [*Pterocles senegallus*], cream-colored courser [*Cursorius cursor*]; Dean 2004)	Irruptions (e.g., waxwings [*Bombycilla garrulus*], crossbills [*Loxia* spp.], jays [*Garrulus glandarius*]); overshooting (e.g., quails [*Coturnix coturnix*], black redstarts [*Phoenicurus ochruros*]); nomadism

the processes that bring about seasonal changes are exploited by migrants to help them on their journeys. The atmospheric conditions in a particular hour, day, or week will influence the timing and duration of the individual movements. In some cases weather conditions will assist passage, but in others they may hamper it or prove to be fatal. Bird irruptions—sudden arrivals of many individuals of usually scarce fruit- and seed-eating species—are often due to cold-weather movements brought on by a combination of high population levels and a lack of available food in the source area. Cold-weather movements in general can be caused by the sudden freezing of water bodies, by falls of thick snow covering feeding areas, or by frost hardening the ground (table 1; Elkins 2005).

Migratory connectivity

Developments in the applications of satellite telemetry (Gillespie 2001, Nathan et al. 2003), molecular genetics (Sunnucks 2000, Nathan et al. 2003), and stable isotopes (Hobson 2005) are now leading to elucidation of the links between migrant populations at different times of their life cycles. "Migratory connectivity" is the term coined to describe movements of individuals between summer and winter populations, including intermediate stopover sites en route (Webster et al. 2002). This connectivity is now being assessed quantitatively by examining the extent to which individuals from the same breeding area migrate to the same nonbreeding area, and vice versa.

For instance, by "leapfrogging" over other birds' winter destinations, some birds from the most northern parts of a summer breeding range may spend their winters in areas farther south than the winter destinations of birds that breed south of them in the summer quarters. Clegg and colleagues (2003) used genetic markers (microsatellites) and hydrogen isotope ratios to find evidence in support of the hypothesis of a leapfrog migration in Wilson's warbler (*Wilsonia pusilla*). Birds from the northernmost breeding areas in North America were overwintering at the most southerly locations in Central America.

Furthermore, Clegg and colleagues (2003) found evidence that, among western birds, coastal breeders overwintered in western Mexico, but those breeding farther inland and at high elevations overwintered in eastern Mexico. Similarly, willow warblers (*Phylloscopus trochilus*) that breed in southern Sweden overwinter in West Africa, whereas those breeding in northern Sweden spend their winters in central or southern Africa (Hedenström and Pettersson 1987, Chamberlain et al. 2000). This is an example of a "migratory divide," whereby migrant populations split, often into western and eastern subpopulations, with one group traveling to its winter quarters via a western route and the others taking an eastern path. A classic case of a migratory divide is provided by European white storks (*Ciconia ciconia*), which, depending on the longitude of their breeding locations, travel around the Mediterranean Sea either via Iberia and the Strait of Gibraltar in the west or via the eastern coast. In the willow warbler example, the migratory divide is associated with a hybrid zone between *P. trochilus trochilus* and *P. trochilus acredula* and is typical of many species in the Palaearctic–Afrotropical migration systems that retain philopatry in both breeding and wintering areas.

Carry-over effects

Events that occur in one season but influence individual success in the following season are known as "carry-over effects." For instance, American redstarts (*Setophaga ruticilla*) coming from high-quality tropical winter habitat arrive earlier and have higher reproductive success in their temperate breeding areas than do individuals coming from low-quality winter habitat (Marra et al. 1998, Norris et al. 2004). Similarly, black-tailed godwits (*Limosa limosa*) arriving early on their Icelandic breeding grounds were more likely to have come from higher-quality habitat the previous winter (Gill et al. 2001). Norris (2005) argued that carry-over effects are important in the population dynamics of such migratory species and modeled the effect of winter habitat loss on equilibrium population size.

Metapopulations

It is easy to think of the simple classification in table 1 as describing members of a population that move to suitable habitats where their conspecifics were absent at the outset, but this is not always the case. This is illustrated by the mixing, including genetic mixing, that occurs within metapopulations. These are defined as populations consisting of linked subpopulations, and the mixing between the subpopulations has important consequences for population processes. Levins (1969) envisaged a metapopulation as a population of unstable local populations inhabiting discrete habitat patches (Levins 1969, 1970, Hanski 1998). Thus, the concept of metapopulations as a set or constellation of local populations that are linked by dispersal (Gilpin and Hanski 1991) is inextricably associated with movements, but not always with migration as such. Rates of dispersal from one local population to another within a metapopulation may determine extinction and recolonization of patches, and the particular individuals involved in recolonization events will determine the genetic makeup of new local populations (the founder effect). Hence "dispersal is the glue that binds together the components of a metapopulation, causing the demographic interconnection that is essential to metapopulation dynamics" (Winkler 2005). The metapopulation idea helps to interpret migration behavior when the animals concerned are moving not from a fixed source to a fixed destination, but from a variety of sources to a variety of destinations, each of which may or may not have been visited before by the animals involved. In the cases of the quelea birds and locusts discussed below, which sources and which destinations (the local populations of the metapopulation) become involved in migration events in a particular season will depend on that season's environmental conditions in relation to what happened during the previous season. Thus the metapopulation approach, together with novel data from molecular tools and other new techniques in combination with modeling, assists in finding patterns among seemingly disparate and apparently random movements that until recently defied prediction.

Migrant pests as metapopulations

The migrations of two species, red-billed quelea birds (*Q. quelea*) and desert locusts (*S. gregaria*), have been studied in detail because they are serious pests capable of devastating crops, especially when they occur at extremely high densities. Our knowledge of their movements provides the best examples of migrations within the Afrotropical region, although the desert locust's migrations also involve the Middle East and Asia.

We suggest that these species, both of which are found in unstable local populations in discrete habitat patches, can be considered as metapopulations, the dynamics of which are strongly influenced by dispersal and migration phenomena and driven by environmental fluctuations. Classic examples of metapopulation dynamics involve extinctions of low-density local populations attributable to habitat changes resulting from a variety of local causes or to stochastic events that had led to poor reproductive success or had induced emigration. In contrast, extinctions of local populations of locusts and quelea birds may involve the disappearance of very high population densities as a result of natural environmental events associated with seasonal rainfall patterns (or even control activities undertaken by humans), with local extinctions being part and parcel of their migratory syndrome.

Migrations of the red-billed quelea

Although *Q. quelea* do sometimes return to "traditional" roosting or breeding sites, their migration pathways differ from year to year, as their movements are determined by rainfall patterns occurring in a particular season (Ward 1971). Nevertheless, their displacements are migratory rather than nomadic, because, before moving, they lay down fat deposits in amounts that are correlated with the distances eventually travelled (Ward and Jones 1977); they make long, straight flights; they fly over areas that are apparently suitable at the time but may not be so when the birds are ready to breed; and, at least in one subspecies, a migratory divide is involved.

In southern Africa, the bird is represented by the subspecies *Q. quelea lathamii,* which has a migratory divide across a southwest-to-northeast axis traversing Botswana and Zimbabwe at an angle of about 27 degrees (°) to the east, relative to the north–south perpendicular line. The birds spend their dry seasons either north or south of the divide, moving toward it as the rain fronts dictate and then receding from it as the dry periods return (figure 1). Given that birds caught in Zimbabwe at the end of the dry season were predisposed to migrate either northwestward or southeastward (Dallimer and Jones 2002), some genetic differentiation and incipient subspeciation might be expected as part of a mechanism that keeps subpopulations apart in the dry seasons. But, on the contrary, morphological studies (Jones et al. 2002) and analyses of DNA microsatellites (Dallimer et al. 2003) from birds on both sides of the divide showed no significant evidence of genetic differentiation, supporting the hypothesis of a single interbreeding population. The implication is that genetic mixing takes place when the birds from different subpopulations meet in the wet season, and the low levels of differentiation may reflect the lack of constancy in breeding sites, which contrasts with the marked philopatry of *Phylloscopus* species.

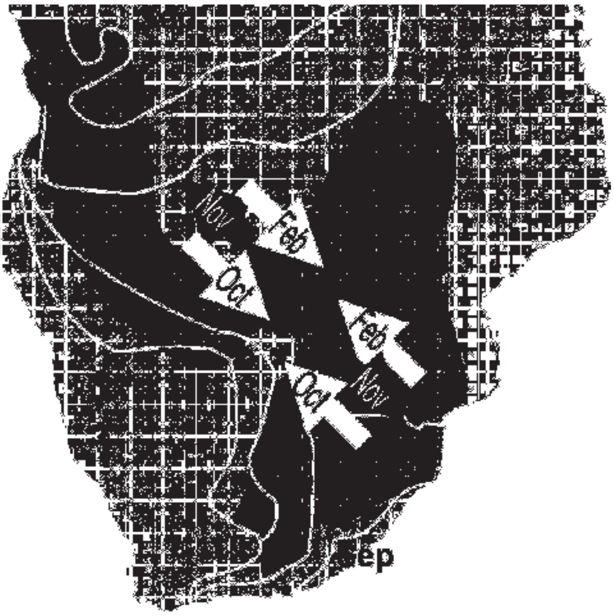

*Figure 1. Likely directions and times of red-billed quelea (*Quelea quelea lathamii*) migrations in southern Africa. Shaded part represents the bird's geographical range, and lines show the start of the wet season. In October, movements are ahead of rain fronts, concentrating birds in the center of the region. When the rain fronts join, birds move back over them (in November) to the southeast or the northwest (migratory divide). Later they breed and, in February, return toward the center of the region. Adapted from Dallimer and colleagues (2003).*

The low incidence of philopatry in *Quelea* is probably a consequence of the environmental heterogeneity that determines where and when the birds can breed, leading to different patterns of breeding-site distributions in different years. For instance, during the 1999–2000 season, 224 *Quelea* breeding colonies were reported from Botswana, but in 2004–2005, there were none in that country. Environmental variation drives the migrations, as these predominantly granivorous birds would starve if they remained where sufficient rainfall (> 60–70 mm within 10 days) had led to seed germination. They therefore travel in front of the rain to areas where seeds remain on the ground from the previous season. When rain then reaches these destinations, they fly back in their "early-rains migrations" to zones where the first new flushes have already produced new seeds and they can begin to breed (Ward 1971, Ward and Jones 1977). Later, they travel on "breeding migrations" to where adequate rain (> 300 mm since October; Venn et al. 2003, Cheke et al. 2007) has made conditions good enough for them to breed again, and they may nest a third time in one season.

The way in which such rainfall regimes and their varied spatial patterns determine different migration patterns can be illustrated by the contrasting examples of the three consecutive seasons of 1965–1966, 1966–1967, and 1967–1968, illustrated in figure 2. In 1965–1966, breeding began in Mozambique in December; by January, it was concentrated along the South Africa–Mozambique border, southwest of the initial sites. By February, the birds spread around Mozambique in a northeastward shift, and by March all activity was in the Francistown region of Botswana, where breeding would have been facilitated by the heavy rain (249 mm) recorded there during February. In 1966–1967, breeding began following substantial rain in South Africa before December (254 mm at Pretoria in October and November), with the heavy rain in Botswana during that month (253 mm at Francistown) allowing widespread breeding there in January and February. There were drought conditions throughout much of the region during 1967–1968, but following initial breeding in South Africa, rainfall was sufficient only to permit widespread breeding in Mozambique, with rainfall in Botswana inadequate and too late (only 25, 58, and 54 mm at Francistown in December, January, and February, respectively), so no breeding occurred there that season, as in 2004–2005. These differences were attributable to variation in the spatiotemporal patterns of rainfall in the zone, which can be used to model where and when the birds can breed (Venn et al. 2003, Cheke et al. 2007) and, given correlations between austral summer rainfall and numbers of colonies reported, the likelihood of their populations being high.

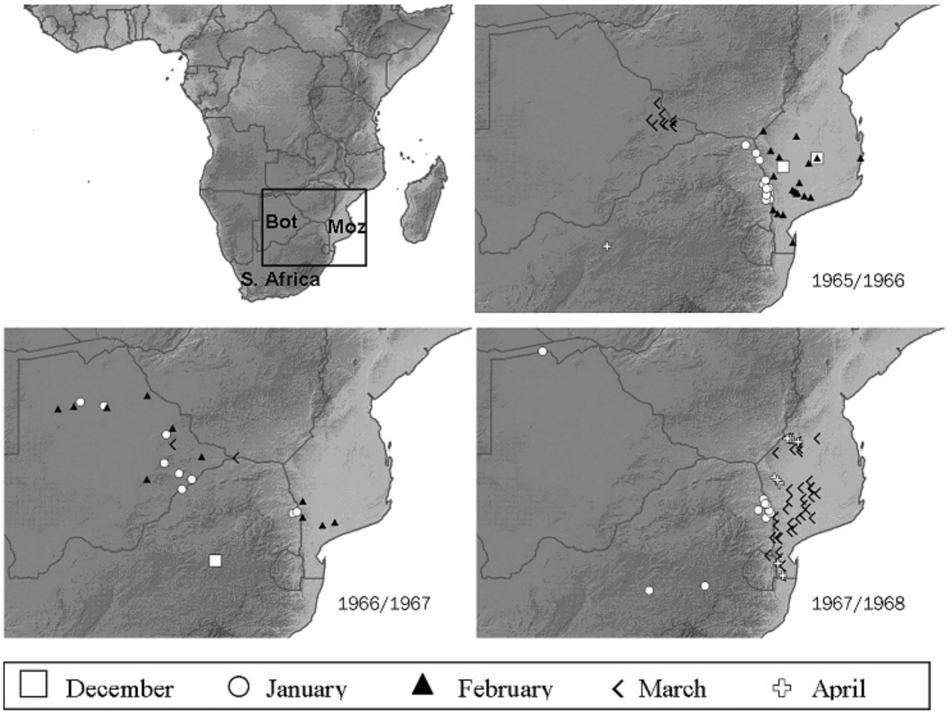

*Figure 2. Locations of breeding colonies of the red-billed quelea (***Quelea quelea lathamii***) recorded in different months in southern Africa (inset) in 1965–1966, 1966–1967, and 1967–1968. Abbreviations: Bot, Botswana; Moz, Mozambique; S. Africa, South Africa.*

Migrations of the desert locust

Insects as well as birds have been used as the subject of studies of connectivity. For instance, stable isotopes are being used to elucidate connectivity among populations of monarch butterflies (Hobson et al. 1999, Dockx et al. 2004) and would be appropriate for studying migrant pests with phase change. Locusts, and moths such the African armyworm (*Spodoptera exempta*), are unusual in that they undergo density-dependent phase changes, involving alterations in their morphology, physiology, and behavior. When "solitarious," locusts behave like ordinary grasshoppers and do not swarm, but when their populations reach a threshold density they gradually change to become "gregarious" during a process known as gregarization: Their color changes, their hoppers march together, and the adults swarm and migrate by day instead of at night. When solitarious, the locusts occur within a "recession area," but gregarious, swarming locusts can move into and occupy anywhere within a much larger "invasion area" during plagues (figure 3). Furthermore, swarming insects usually move downwind in such a way that convergent winds will take them to where it is raining (Rainey 1951). Thus the migratory behavior following a phase change is an adaptation allowing migrants of this sort to survive in spatiotemporally variable habitats: When there is ample rain, migrations will take the insects to patches of green vegetation for feeding and to habitats damp enough for them to lay eggs. However, reliance on downwind movements is not the whole story. In some cases, such as after northward movements across the Sahara in autumn, the prevailing winds (northeasterlies in this case) would blow the insects back in the wrong direction. The locusts are adapted not to take off under such conditions, perhaps because the northeasterlies are too cold. Similarly, locusts in central Saudi Arabia in the early summer reach central Sudan by crossing the Red Sea but do so by waiting for one of the few days when northeasterly upper-air winds are blowing at the correct height for the journey, eschewing take-off during other circumstances (Symmons and Cressman 2001).

To aid understanding of the role of these changes and the involvement of migration in the population dynamics of insects with phase change, modeling approaches have been

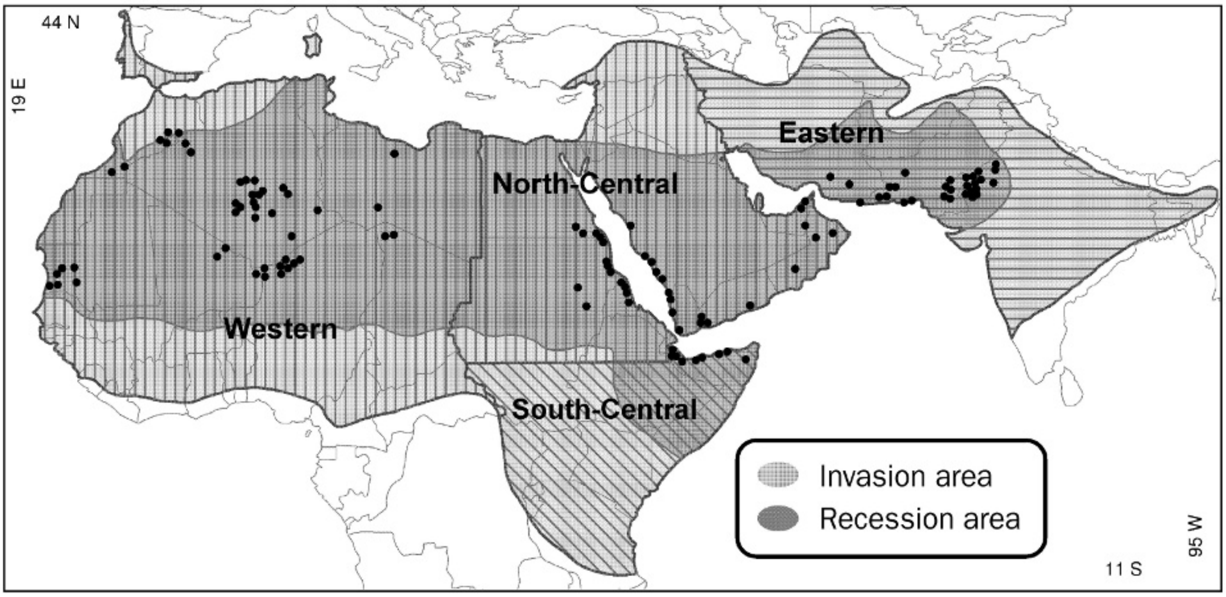

Figure 3. The four desert locust regions, their positions within the areas of desert locust invasion and recession, and the locations of sites (black dots) where gregarization has been recorded.

helpful, particularly for the desert locust (Holt and Cheke 1996, Ibrahim 2001, Tratalos 2001), which has nonlinear dynamics and so, depending on birth and death rates, might exhibit chaotic dynamics. However, analyses of monthly time series of data on numbers of territories infested by locusts were equivocal about chaotic properties (Cheke and Holt 1993, 1996, Holt and Cheke 1996) but did reveal significant autocorrelations at lag 1. This was also the case for the very long series (1001 years) on the Chinese migratory locust (*Locusta migratoria manilensis*) discussed by Sugihara (1995). Thus, numbers in one year are dependent on the numbers in the previous year. However, this is not so for a time series of the brown locust *Locustana pardalina,* which lacks significant autocorrelations (Tratalos 2001, Todd et al. 2002). This species may be under less pressure to migrate because it has a complex means of surviving dry periods, involving egg diapause and quiescence (Matthée 1951). Neither the desert locust nor the Chinese migratory locust has such abilities, although it has been suggested that adult solitary desert locusts can survive unfavorable conditions for 180 days and gregarious adults for up to 230 days after fledging (G. B. Popov, cited in Duranton and Lecoq 1990). The brown locust does migrate, but its movements encompass a smaller area than those of the other two species mentioned above.

An alternative approach is to analyze the links between local populations rather than the populations as a whole. In figure 3, the geographical range of the desert locust has been split into western, north-central, south-central, and eastern regions (see Pedgley 1981). These are not arbitrary but reflect breeding areas of gregarious populations during plagues, which will have emerged from one or the other of the gregarization zones that support populations of solitarious insects during recessions (periods when there is no plague; figure 3 also shows sites where gregarization has been recorded). Thus each zone can be thought of as a local population of a metapopulation stretching from the Atlantic coast of West Africa to Bangladesh. Predictions from the theory of metapopulation dynamics (e.g., that migration can alter population dynamics qualitatively; Hanski 1999) are not always easy to substantiate with field data, but autocorrelations between local populations, such as spatial autocorrelations reported for the American pika (Smith and Gilpin 1997) and the ecology of the Glanville fritillary (*Meltaea cinxia*) (Hanski et al. 2006), provide support for the theory. For desert locusts, analyses of this kind are complicated by seasonality, as different zones support breeding at different times of the year. Similarly, the direction of movements will change with the season (Roffey and Waloff 1981). In spring (March to June), locusts may be found breeding in the North African parts of the western region, but seldom during the summer (August to October) or winter (October to January). Such insects will move southwestward or southward and may meet populations originating from the north-central region and traveling westward, all of which may breed in the Sahel during summer. Similar characteristic breeding times and directions of movements are known for all the other regions that can be interlinked when the insects are gregarious (table 2; Roffey and Waloff 1981).

The paucity of data on solitarious desert locusts and their habit of moving unseen by night (as opposed to the daytime movements of swarms) make it difficult to validate theoretical models, but some insights can be gained from a new spatiotemporal data set on swarming, gregarious populations, based on unit sample sizes (degree squares). Time series of the monthly number of 1° grid squares reported as

Table 2. Movements of desert locusts within and between different regions in the two seasons after breeding, broken down by breeding region and season.

	Movements after breeding, by breeding region			
Breeding season	**Western**	**North-central**	**South-central**	**Eastern**
Summer (August to October)	W or NW within region, veering E (northern circuit) or SE and E (southern circuit); **E into north-central region**	E and N in western part of region; **E across Arabian Gulf into eastern region, S or SE into south-central region**	SE within region	N within region; E within region or **E or SE into north-central region**
Winter (November to January)	N or S from western edge, then veering NE or SE within region; **E into north-central region**	N within region or **NE into eastern region**	Circulating within region or **NW into north-central region**	N or W within region
Spring (March to June)	SW, S, and SE within region; **E into north-central region**	**W into western or E into eastern region;** S or SE within region	Circulating within region or **NW into north-central region**	E within region or W from eastern extremity within region

E, east; N, north; NE, northeast; NW, northwest; S, south; SE, southeast; SW, southwest; W, west.
Note: Interregional movements are highlighted in bold.
Source: Roffey and Waloff 1981.

infested with desert locust swarms, 1930–1987, throughout the desert locust distribution area (referred to as "all-regions" data), and on equivalent series for each of the desert locust regions (western, north-central, south-central, and eastern; figure 3), were collated from the FAO (Food and Agriculture Organization of the United Nations) SWARMS (Schistocerca Warning Management Sysem) data set, described by Magor and Pender (1997).

The time series for the all-regions data shows peaks and troughs corresponding with plagues and recessions (figure 4). But as far as the theme of connectivity is concerned, we are interested here in how the various local populations in the different regions are linked. The four regions have similar cycles, with the eastern and north-central regions often, but not always, leading a sequence when values increased from very low to high values (figure 4). There is also seasonality in the data, with most swarms in May and June, but with different regions contributing differently according to month (figure 5). There was a high degree of cross-correlation between all the regions, with the weakest correlations (but many still significant at the 95% confidence level) generally between the western and eastern regions and between the south-central and eastern regions, and the strongest between the north-central and south-central regions (figure 6). In all cases, the strongest cross-correlations between pairs of regions were for positive or negative lags (e.g., four months between the west and south-central regions or two months between the north-central and south-central regions). If the strongest cross-correlations were for unlagged data, it would indicate that the populations could have been responding to some covarying environmental factors, but this would be unlikely, since the rainfall regimes differ between regions. Thus there is clear statistical evidence that the locusts in different regions are linked, and these geographical units, delineated on ecologically based subdivisions of the invasion area, can therefore be considered as local populations of a huge metapopulation, as suggested above. Proof that they are genetically interlinked will be necessary to put research on their connectivity on the same level as the data already gleaned for birds, but a related question, posed by Ibrahim and colleagues (2000), concerns whether recession populations are remnants of past swarms. On the basis of a nuclear DNA marker (part of the antennapedia-class homeobox gene), there is significant genetic divergence among solitary desert locusts along the Red Sea coast in Eritrea (Ibrahim et al. 2000), possibly maintained by repeated extinction and recolonization in metapopulations, a conclusion supported by Monte Carlo simulation modeling (Ibrahim 2001). The SWARMS data set could also be

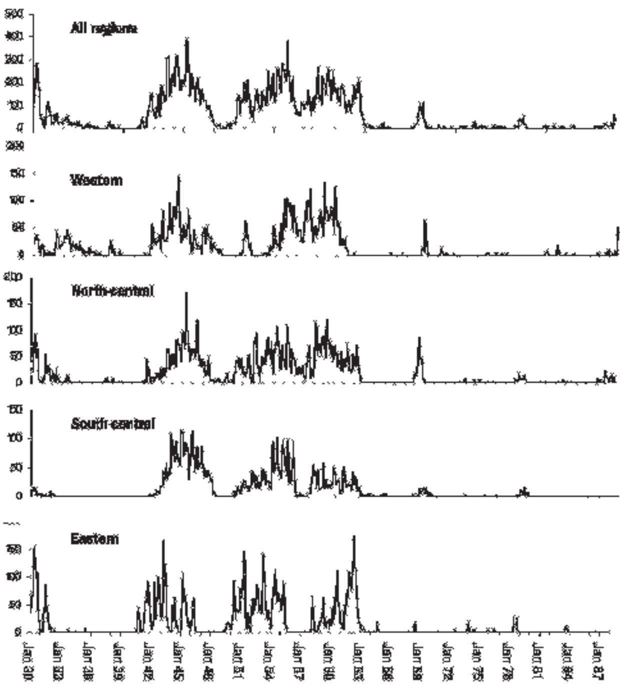

Figure 4. Time series of the monthly number of 1-degree grid squares reported as infested with swarms in the whole desert locust distribution area and in each of the four regions, 1930–1987.

analyzed in more detail, according to colonization and extinction rates in smaller areas, for instance, to examine the connectance within the metapopulation by calculating indices of connectivity (e.g., S_i; Hanski 1998) of patches within the local populations. However, this kind of analysis would be hampered by the need for data on population sizes within the patches, which are often lacking.

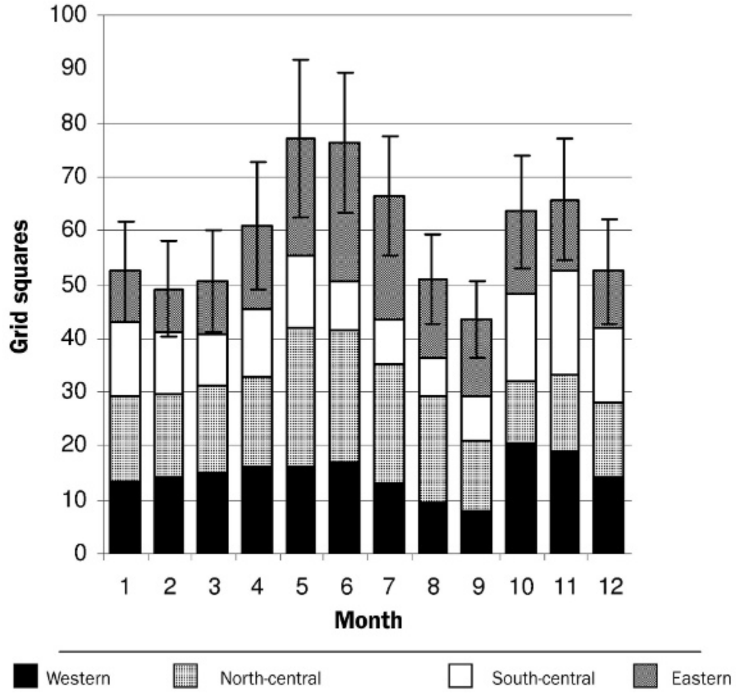

Figure 5. Mean number of 1-degree grid squares reported as infested with desert locust swarms, by month and by region, 1930–1987. Error bars show +/– 2 SE (standard error) for the sum of the four regions.

Conclusions

As Dingle and Drake (2007) point out, migration is a complex process. Migrating insects and birds are adapted to respond to environmental changes, and their subpopulations interlink over distances of thousands of kilometers. Such connectivity and consequent carry-over effects fashion these organisms' survival and shape evolutionary processes in concert with environmental constraints, particularly rainfall and wind directions. These will alter with climatic changes, with implications for migratory behavior in the future. For the major migratory pest species, such the desert locust and quelea bird discussed here, such changes might lead to greater threats to food security in regions where rainfall is expected to rise, but to less threat elsewhere. According to Hulme and colleagues (2001), December–February rainfall is likely to decline in southern Africa to the detriment of the quelea birds, but increased precipitation in June–August in some of the gregarization zones in the central Sahara would benefit the desert locust. In both cases, radical climatic changes are likely to lead to changes in the migratory strategies of the animals, and, being preadapted to coping with environmental uncertainties, these species will probably respond adequately. In contrast, there is already evidence suggesting that Palaearctic–Afrotropical migrants such as the pied flycatcher (*Ficedula hypoleuca*) are failing to match changes in the timing of their breeding with climate-induced changes in the phenologies of their preferred prey insects and are suffering population declines as a result (Both and Visser 2001, Both et al. 2006).

The examples described illustrate how predicting the details of future ecological changes will require greater understanding of the population dynamics and genetic compositions of the organisms in question before we

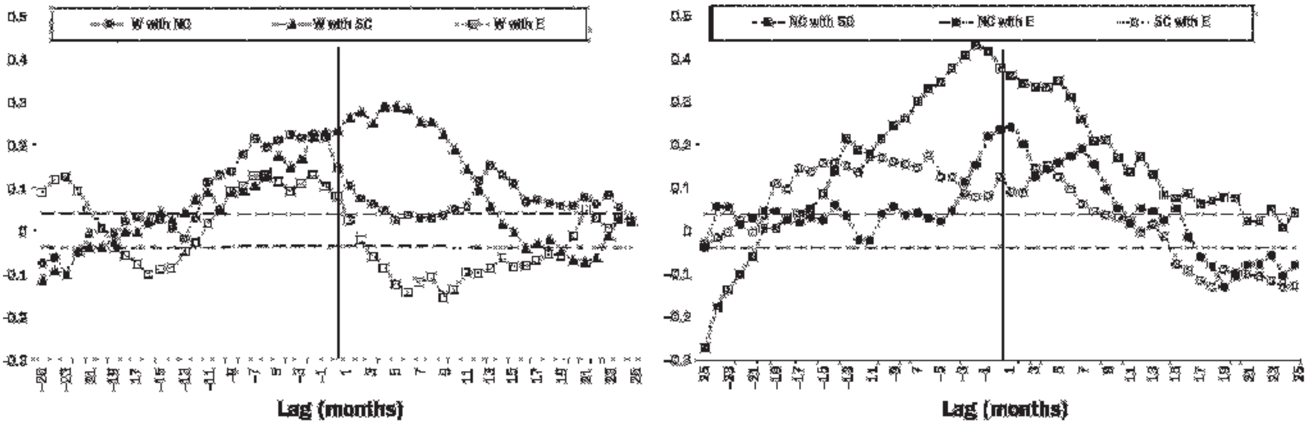

Figure 6. Cross-correlation functions (y-axis gives coefficients; x-axis gives lags in months) of the monthly number of 1-degree grid squares reported as infested with desert locust swarms, 1930–1987, by region. Data were seasonally differenced. The gray dashed horizontal lines indicate 95% confidence intervals, and the vertical lines show the position of cross-correlations with zero lag. Abbreviations: E, eastern region; NC, north-central region; SC, south-central region; W, western region.

can fully appreciate the selective advantages of different strategies and their evolution in relation to climatic variability. Chance, the patchiness of rainfall, and the vagaries of wind speeds and directions all impinge on the biology of migratory organisms, especially in arid or semiarid ecosystems. Further work is required on the extent of genetic links between different populations of both locusts and quelea birds, and on how these migrants detect where rainfall will be adequate for their needs. This would help to elucidate the maintenance of connectivity, the mechanisms involved in how these species make decisions on directions of travel, and any as yet undiscovered carry-over effects.

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