Biological Characteristics of Invaders among Bird Species in Britain [and Discussion]

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Biological characteristics of invaders among bird species in Britain

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Among Western Palaearctic birds, range expansion is more commonly observed in families with low proportions of long-distance migrants than among generally migratory families. Migrants are also disproportionately scarce in the Irish avifauna, compared with that of Britain, and scarcer among colonists of Britain than among long-established species. Colonization attempts in southeast England and in Scotland have more frequently resulted in establishment by the invader than have attempts in areas more remote from the European mainland; in several cases, these attempts have followed a history of range expansion and/or population increase in the source areas. Successful colonists lay more eggs each season, on average, than failed colonists; this difference is due, in part, to larger clutches and in part to more clutches per season. The failure of migrants to make successful invaders is attributed to their inability to compete for resources, especially habitat, in the face of competition from year-round residents. The findings otherwise agree well with predictions of the MacArthur–Wilson theory of island colonization.

Introduction

The study of biological invasions tends, not unnaturally, to be dominated by case studies of successful invaders that have come to have a major role within the receiving community. Studies thus based therefore tend to emphasize the characteristics of success at invasion, with relatively little emphasis on the characteristics of failed invaders; such characteristics are, by definition, difficult to study because of the paucity of data concerning them. In bird species invading Britain and Ireland, however, the record of potential invaders is quite well documented (see, for example, Sharrock & Sharrock 1976). Most birdwatchers are fascinated by rarities; some are willing to travel enormous distances for sight of a rarity not previously within their experience. This degree of commitment, together with the large numbers of birdwatchers involved, has resulted in quite comprehensive coverage of the arrival and subsequent fortunes of unusual birds reaching Britain and, to a lesser extent, Ireland. Information on breeding attempts by invading species is much less in the public domain, largely because of concern about the risk to the species from egg collectors and, in raptorial species, from illegal falconry. The available record of additions of new species to the recognized avifauna of Britain nevertheless provides a useful source of historical record from which to evaluate biological characteristics of invading bird species.

Islands also provide particularly good examples of invasions by birds (MacArthur & Wilson 1967); their separation from the mainland source avifaunas allows the ready delineation of the avifauna on the island, and requires discrete colonizing events rather than simple range expansion (i.e. incorporation of adjacent land into the species range). MacArthur & Wilson (1967) and MacArthur (1972) developed an important body of island biogeography theory that is relevant to successful colonization of new islands. Their theoretical treatment emphasizes three elements. First, for successful colonization to occur, the species concerned must be able to reach the island from the mainland source population. Secondly, small populations are extremely vulnerable to extinction through stochastic events, so that the larger the founder population, the greater its chances of establishing itself. Thirdly, a founder population with a large, rather than small, rate of population increase is more likely to grow past the vulnerable stages of early colonization. This rate of increase is the difference between birth rate per head and death rate per head; and any given rate of increase can be achieved either as a difference between a large birth rate and a large death rate or as a difference between a small birth rate and a small death rate. MacArthur (1972) identifies the latter as the safer option, and also notes that populations that are constrained to some low level (some tens or hundreds of pairs) are more vulnerable to random extinction than are larger populations of hundreds or thousands of pairs. Extinctions of small populations may be brought about by random population fluctuations, by competition, or by predation (including disease) and, although the last two are often density-dependent and therefore weaker at low densities, they can reduce the populations to levels where random population fluctuations can drive the species to extinction (MacArthur & Wilson 1967). The validity of these ideas within the British avifauna is the major issue addressed in the present paper.

Materials and methods

Data for the present study were drawn from two sources. First, the annual reports of the Rare Breeding Birds Panel (RBBP) for the ten years 1973–82 were used as a source of data on currently rare breeding birds, some of which were newly arrived species but others of which are declining species. The Rare Breeding Birds Panel is an *ad hoc* body, which receives, on a confidential basis, records of breeding by rare species and which maintains the records concerned against the day when successful invasion and spread or adequate evidence of total failure of the invasion allows the material to become part of the historical record. The Panel publishes annual reports (e.g. Spencer *et al.* (1985)) summarizing the current status of the species within the Panel's remit. Such reports are not comprehensive, particularly as some local ornithological societies do not contribute records to the Panel's files, but nevertheless provide much useful information on the developing status of invaders and would-be invaders. Second, the list of RBBP species was enlarged to include other species that are now common but known to have colonized Britain within the last 200 years. Some of these colonizations are known to be recolonizations by species whose British populations had become extinct; other are either new colonists or are species that died out before the modern historical record. For the present paper, introduced species are not considered. The inclusion in the data set of the non-invader native rarities on the RBBP list provided a convenient sample of species with populations of the sizes experienced by invaders during the early years of their invasions.

Results

Migratory behaviour and invasive probability

The theory of island biogeography assumes that isolated islands are quite frequently reached by individuals of species not already present on the island, thus providing the raw material for potential colonization. MacArthur & Wilson (1967) explored the consequences of altering the frequency of such arrivals. For example, they considered the effects of a reduction in arrival rate, as when the colonization of remote islands is compared with that on islands near to mainland sources, and of a change in island size, as when the colonization of small islands is compared with colonization of larger islands when both are equidistant from the mainland. MacArthur & Wilson (1967) do not expressly consider the relative impact of migratory versus sedentary habits on the probability of colonization of islands by birds, though their arguments *vis-à-vis* effects of remoteness and of island area are arguably more appropriate to populations diffusing out from a central source population than to migratory species following defined flyways. In practice, however, islands close to continental flyways often experience the arrival of large numbers of migratory individuals that have been drifted off their normal route by lateral winds. For example, bird observatories along the east coast of Britain regularly experience inundations of drift migrants that have been displaced westwards from the normal passage route between southern Europe and Fenno-Scandinavia in spring, and even more so on the reverse route in autumn. Similarly, southwestern locations in Ireland (e.g. Akeragh Lough) and Britain (e.g. the Scilly Isles) regularly receive North American migrants that have been drifted eastwards. This phenomenon of drift migration (for review see Williamson 1969) thus regularly brings large numbers of migrant individuals into areas in which they do not regularly breed. Were arrival rates the major factor contributing to successful invasion of new areas, one would therefore expect to find long-distance migration a characteristic of successful invaders. A contrary argument, however, is that individuals born to parents that have arrived by chance in these new areas are unlikely to abandon their ancestral migratory habits abruptly. The high degree of subsequent success in returning to their natal areas then demanded of these offspring may be more demanding than would be the maintenance of relatively sedentary behaviour on the part of non-migratory individuals reaching those same areas by chance. Logical arguments are thus somewhat equivocal about the relative importance of migratory and sedentary behaviour in promoting invasion of new areas.

The possibility that migratory behaviour contributes to the probability of successful invasion of new areas can be examined in a number of ways, mostly indirect. First, one might expect that migratory species would contribute disproportionately to range expansions. Table 1, however, shows that among the western Palaearctic passerines documented by Harrison (1982) the proportion of species undergoing range changes is very similar among fully migrant species and among wholly resident species: only 7 of the 95 migrant species and 6 of the 86 resident species are listed as undergoing range changes (overwhelmingly of range expansion). Although Harrison's instancing of range expansions may well be incomplete and is biased towards the better-documented or more pronounced cases, there is no *a priori* reason to expect a bias towards or against migrant species, so the analysis here suggests no particular propensity on the part of migrants towards range expansion. This analysis does not consider, however, the role of species in which some populations are completely migratory and other populations are completely resident. For example, northern and northeastern European populations of the willow tit, *Parus montanus*, and blue tit, *P. caeruleus*, respectively normally vacate their breeding grounds completely in winter, even though elsewhere populations of these two species are completely resident (Harrison 1982). When species with such migratory populations are added to the analysis, a bias against migrants successfully expanding their ranges becomes apparent (figure 1). The figure plots, for Western Palaearctic passerine families, the relative frequency of range changes in each family against the relative frequency of fully migratory populations

Table 1. Occurrence of range changes and of migrant species within passerine bird families within the western Palaearctic

(Based on data in Harrison (1982).)

family	number of species		undergoing range change
	total	migrant[a]	
larks, Alaudidae	22	2	*
swallows and martins, Hirundinidae	9	5	
pipits and wagtails, Motacillidae	14	8	
waxwings and hypocolius, Bombycillidae	2	0	
bulbuls, Pycnonotidae	2	0	
shrikes, Laniidae	8	4	
dunnocks, Prunellidae	6	1	
warblers, Sylviidae	57	41	*
flycatchers, Muscicapidae	4	4	*
thrushes, etc., Turdidae	41	16	*
babblers, Timaliidae	5	0	*
long-tailed tits, Aegithalidae	1	0	
penduline tits, Remizidae	1	0	*
tits, Paridae	9	0	
nuthatches and wallcreepers, Sittidae	7	0	*
treecreepers, Certhiidae	2	0	
dippers, Cinclidae	1	0	
wrens, Troglodytidae	1	0	
sunbirds, Nectariniidae	4	0	
buntings, Emberizidae	18	10	
finches, Fringillidae	30	2	*
waxbills and mannikins, Estrildidae	3	0	
sparrows and snowfinches, Ploceidae	12	1	*
orioles, Oriolidae	1	1	
starlings, Sturnidae	4	0	*
jays, magpies and crows, Corvidae	15	0	*[b]

* Some species in the family undergoing range change.
[a] Number of wholly migrant species.
[b] Two species contracting in range.

(not species) in the family concerned and shows a general decrease in the proportion of range changes observed as the proportion of migratory species increases. Of the range changes considered here, only two, both involving corvid species, were decreases and their omission does not in fact detract from the general trend that is apparent (figure 1). One may conclude, therefore, that it is the more sedentary families that are likely to undergo range expansions.

The relevance of range expansions to invasions can be questioned, in that range expansion involves the sustained invasion of new areas often immediately adjacent to the existing range. Against this, the range expansion of the collared dove, *Streptopelia decaocto*, during its spread from the Balkans to occupy almost the whole of Europe by the 1970s, is almost universally cited as the most recent classic example of an avian invasion, so the semantics of range expansion against invasion are somewhat pedantic. Even insular studies, however, yield evidence against a major role for migrancy in promoting invasions. Lack (1976) reviewed the relative composition of the British and Irish avifaunas. Ireland supports, as regular members of its avifauna, only some 67% of the land birds breeding in Britain. A further 10 British species (10.4%) breed occasionally in Ireland; 13 (13.5%) were recorded only as non-breeders. A major fraction of the British avifauna has thus failed to invade Ireland successfully. Lack noted

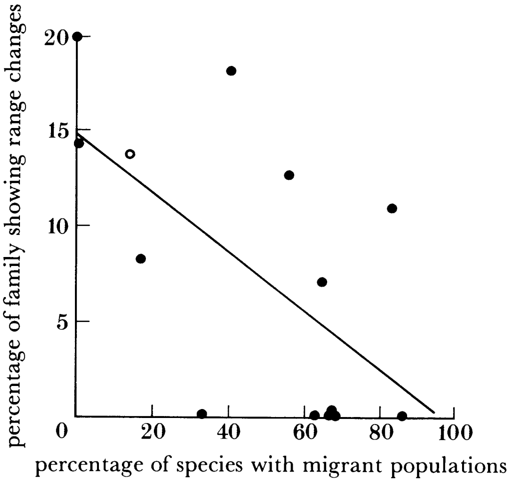

FIGURE 1. The relation of range changes within various passerine families in the Western Palaearctic and the percentage of species within that family that have fully migrant populations. Based on families with five or more species in Harrison (1982). The open circle indicates the Corvidae, the only family recording decrease in range. The regression line is $y = 14.93-0.16x$ ($r = 0.622$).

that if migrancy were significant in promoting invasion, one would expect to find a greater proportion of migrant than of resident British breeders to have colonized Ireland. In fact the proportions observed are biased in favour of resident species: only 16 of the 46 migrant species (35 %) regularly breeding in Britain also breed in Ireland, but 86 of the 125 resident species (69 %) do so. The corresponding analysis has not been performed for the British avifauna in relation to that of northwest Europe, there being major difficulties about defining the relevant source pool of species. I have attempted to bypass such problems by comparison of those species that have successfully invaded or re-colonized Britain in the last 200 years with correspondingly rare resident species (defined as those within the remit of the Rare Breeding Birds Panel that have never died out completely as British breeding species). This analysis implicitly equates persistence with success. The results also show a bias against migrancy among colonists; of the 30 species classified as successful colonists, 5 are long-distance migrants and 6 are passage migrants (species most of whose British occurrences are birds on passage between wintering and breeding grounds elsewhere), for a total of 11 (37 %) migrants, whilst nine of the 12 rare native breeders (75 %) are long-distance migrants ($\chi^2 = 0.20$, not significant). This latter sample is rather biased in being drawn from just the RBBP species but it simplifies problems of classification of migration over the whole of Britain. (Many individuals in Scottish populations move southwards in winter while their southern breeding conspecifics remain resident year-round; for discussion see Prŷs-Jones (1984) and Lack (1986).) The ratio of migrant to resident species is, however, probably very similar across species of very different densities. In a study based on the more abundant species monitored by the BTO's Common Birds Census, some 13 of the 43 species considered (30 %) were long-distance migrants (O'Connor 1981); this ratio is similar to the 37 % of the RBBP species above ($\chi^2 = 0.28$, n.s.).

These three lines of evidence thus suggest that migrancy is not a factor that predisposes a species towards successful invasion of established communities, be they mainland or island ones, and that a predisposition towards residency may be a better precursor of success in invading.

The role of propagule size and repeated invasion

MacArthur & Wilson (1967) emphasized the importance of founder population size in determining the probability of successful colonization of islands. In the simplest case, any invading bird needs a conspecific mate before breeding in the new area is possible. The resulting offspring in turn need to find mates, probably in the face of a high risk of inbreeding. These needs are more easily met if more, rather than fewer, conspecifics have reached the area. The generally low incidence of successful establishment of avian introductions into foreign communities indicates the high risk of extinction of populations started with small propagules. This point is strengthened by the greater success of introductions where the introductory programme has been sustained over some years; examples of records for Britain include that of the red-legged partridge, *Alectoris rufa*, and of the little owl, *Athene noctua* (Sharrock 1976). In both, the initial introductions failed to establish self-sustaining populations, but persistent introduction eventually succeeded in achieving this goal. Such instances indicate that the initial failure was not due solely to ecological factors, such as competition and predation, although these factors may have made it difficult for the initial birds to breed sufficiently successfully to escape the risks of random population extinction associated with very low densities.

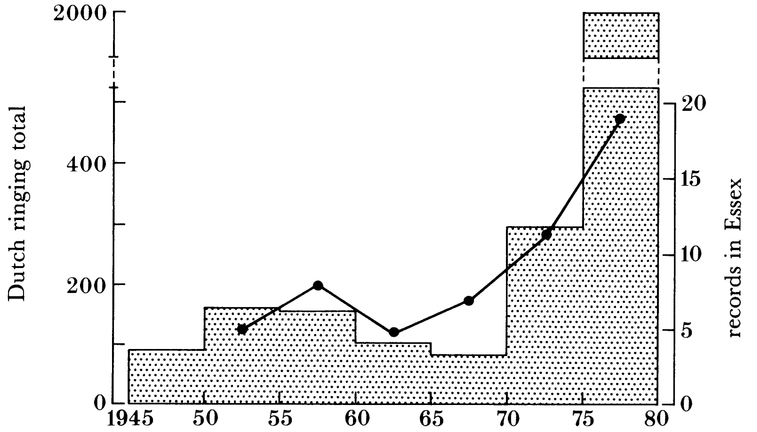

FIGURE 2. The relation between the numbers of marsh harriers, *Circus aeruginosus*, ringed in the Netherlands (histogram) and the number of sightings of this species in Essex (solid line), over each five-year period from 1945 to 1980. Drawn from data in Spencer (1983).

Little is known of the sizes of initial propagules of birds colonizing Britain. At one extreme, some initial colonizations must have been by just one pair, with even the chances of two birds arriving together being remote. The sheer unlikelihood of two spotted sandpipers, *Actitis macularia*, a rare vagrant from North America, reaching the same Scottish location some thousands of miles from their normal haunts has been widely remarked, for example, by Thom (1986). Some 27 species (about one third of all the colonizing events considered here) have bred either just once or only sporadically in Britain in the course of the last 200 years, failing to establish a regular population on the death or disappearance of one or both of the founder pair or, in some cases, of their immediate offspring. No doubt these instances are an underestimate of the frequency of single-pair breeding, the nests concerned going unrecorded (or occasionally unreported) by birdwatchers. Some 30 species have, however, successfully established themselves as regular breeders in Britain since 1800, perhaps aided in some cases by escapes from captive or semi-captive populations (mostly wildfowl and one or two raptorial species) already in the country. Several of these species reached Britain after a history of population increase and range expansion in Europe. The collared dove has already been mentioned, but other examples can be cited, as with Cetti's and Savi's warblers, *Cettia cetti* and *Locustella lusciniodes*; the marsh harrier, *Circus aeruginosus*, provides an example of a return to Britain after population increase in Europe. Figure 2 contains data compiled by Spencer (1983), plotted to show how sightings of marsh harriers in Essex increased in parallel with the increase in numbers in the Netherlands, as evidenced by the Dutch ringing totals. Coastal reclamation has created much new polderland in the Netherlands, providing marsh harriers with additional habitat. The resulting population increase has in turn led to greater dispersal across the North Sea.

The importance of a nearby population source to maintain the colonisation of new areas is suggested by the data of figure 3. The maps show the location of the original invasion sites, where recorded, for three classes of invader: (1) sporadic breeders, species that have been recorded breeding but that have failed to establish regularly breeding populations; (2) recolonists, species that have re-established breeding populations in Britain after the original populations went extinct; and (3) new colonists, species that have newly invaded Britain (though some of these species may have bred in the country in the more distant past, in different climatic and ecological régimes). The distribution of breeding by the first category shows greater geographical spread than do those of the other categories, which are more clearly concentrated into southern and eastern England and into Scotland, i.e. into those parts of the country immediately adjacent to continental and Scandinavian source populations. Although circumstantial, the geographical concentration of the breeding attempts that subsequently gave rise to established populations is suggestive.

The influence of rates of population increase

The model of invasion persistence produced by MacArthur & Wilson (1967) shows that populations with high ratios of birth to death rates are more likely to persist in the face of random population fluctuations than are populations with lower ratios. Lacking information on the survival rates of many invading species, we consider here only the possible influence of birth rates. Figure 4 shows the pattern of seasonal egg production in the various categories of species considered within the data set used here. Species that have successfully invaded Britain have had significantly larger egg production than have species that failed to establish themselves, and these in turn have had more prolific output than have the native species. This last group again comprises only those species on the RBBP list and in this analysis this is arguably a source of bias; species on the RBBP list are by definition rare, which state they may have reached by virtue of reproductive rates too low to permit them to achieve high numbers. O'Connor (1981) has examined the distributions of seasonal egg production among the commoner resident and migrant species in Britain; the pooled distribution of these data does not differ significantly from that found here for successful invaders. The successful invaders thus produce at least as many eggs as the common species already established in the country, they produce more eggs than do unsuccessful invaders, and they produce still more eggs then do the rare native species, many of which may be declining in numbers. Note, though, that the invaders are, at least initially, also rare, so the difference in productivity between rare native species and the newly arrived invaders is probably significant.

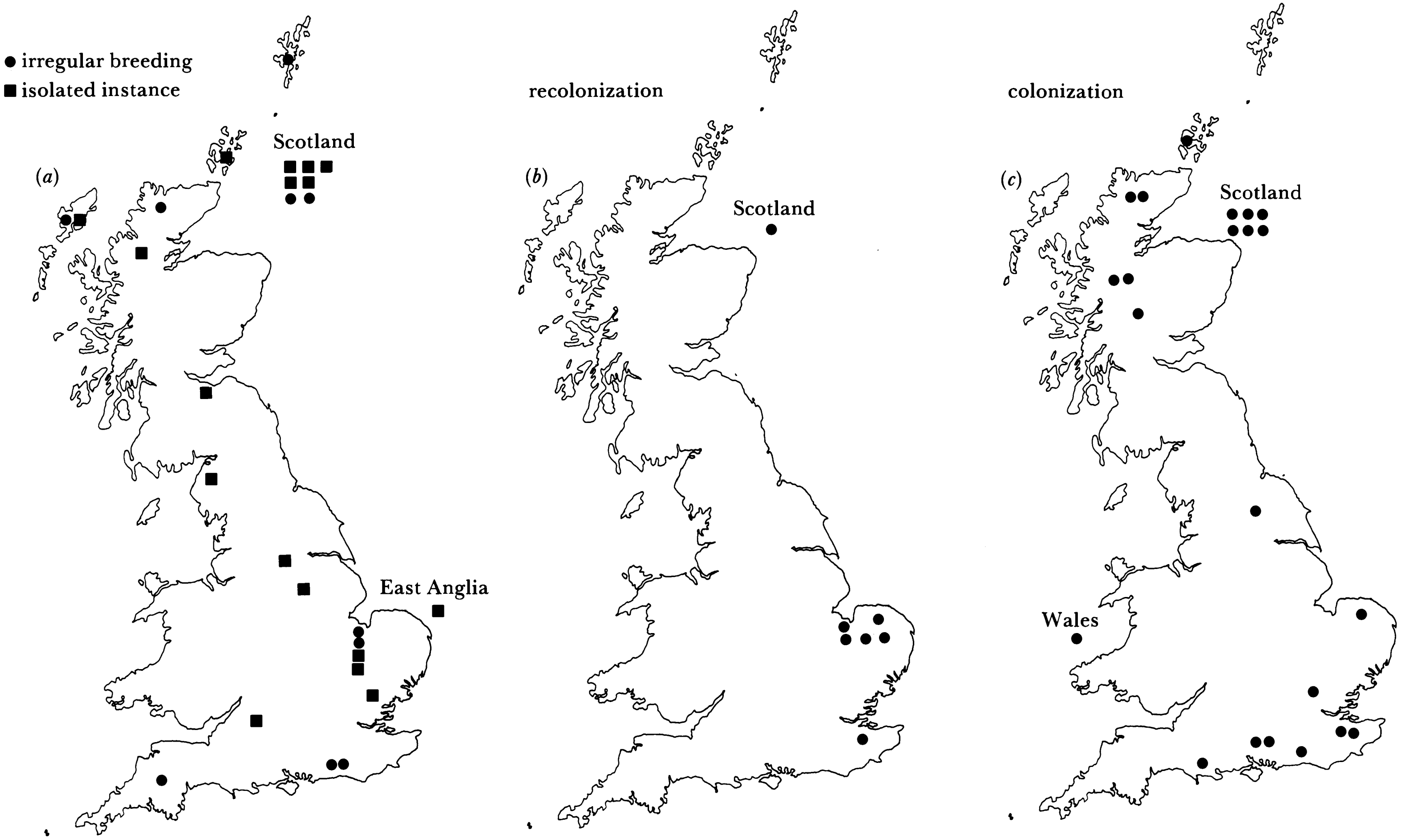

FIGURE 3. The location in Britain of first breeding records of various categories of species: (*a*), sporadic breeders (square symbols indicate sole occurrences of the species concerned); (*b*), re-colonizing species; (*c*), invaders. Points outside the map outline refer to confidential records whose precise location has been withheld.

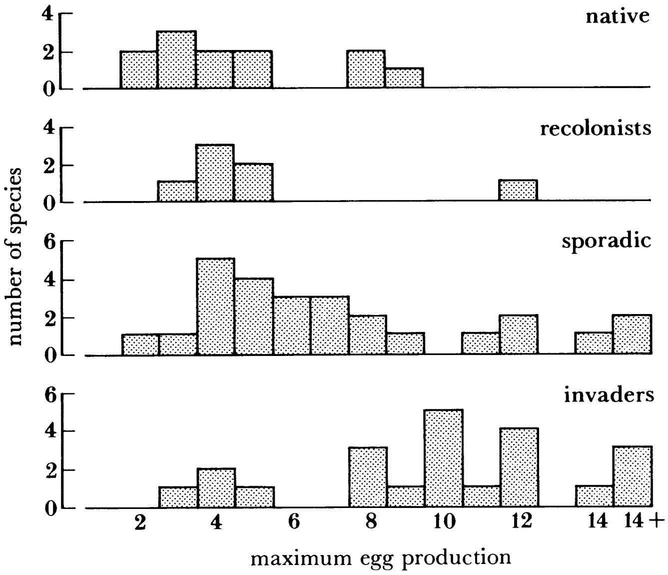

Figure 4. Seasonal egg production in four categories of breeding birds in Britain: (*a*), native species on the Rare Breeding Birds Panel list; (*b*), recolonizing species; (*c*), sporadic breeders that have not established themselves as regular breeders; (*d*), successful invaders. Egg production here was taken as the product of normal maxima of clutch size and broods per season, based on data in Hickling (1983) and Harrison (1975).

It is widely argued that reproductive effort and adult survivorship are inversely related, so that high egg productivity can be achieved only at the cost of greater adult mortality (Cole 1954; Stearns 1976). I have recently questioned this argument as being over-simplistic, for a preliminary analysis of data on egg production rates and adult survival suggests that such trade-offs are prevalent only amongst species that produce their seasonal complement of eggs in a single clutch (O'Connor 1985). In multibrooded species, where the same number of eggs, but spread over several clutches, may be laid each season, survival rates are independent of egg production. If a trade-off of survival against egg production can be avoided in this way, then multi-brooded species should have a greater ratio of birth rate to death rate than have single-brooded species laying the same number of eggs. The MacArthur–Wilson model would then predict that multi-brooded invaders are more likely to establish themselves successfully than are single-brooded species. Table 2 shows that this is indeed true of species invading Britain. The possibility of taxonomic bias in this result was checked by comparing separately the data for passerine and non-passerine species, because non-passerines are often larger species

Table 2. The incidence of multiple broods per season among various categories of bird breeding in Britain

category	number of species: single-brooded	number of species: multi-brooded	percentage multi-brooded
native species[a]	10	2	16.7
recolonists	6	2	25.0
sporadic breeders	18	8	30.8
invaders	9	13	59.2

[a] Species on Rare Breeding Birds Panel list only.

with longer nest cycles and are therefore less likely to attempt more than one brood per season. Multibrooded species remained disproportionately frequent amongst species of the passerine class, but among non-passerines this tendency was weak and not of statistical significance. Finally, it should be noted that the between-class differences in number of broods produced do not account for the whole of the differences of figure 4, for clutch sizes also vary between classes (Kruskal–Wallis oneway analysis of variance $= 8.83$, $P = 0.03$).

Discussion

The results above suggest three main points about invading bird species. First, a propensity for long-distance migration is not advantageous, and may be disadvantageous, in facilitating successful invasion of alien bird communities. Secondly, invasion is likely to be more successful if a source population is nearby to sustain and reinforce the invaders until the new population has become self-sustaining. Thirdly, a high rate of population increase is advantageous, certainly when achieved through high rates of egg production and even more so if produced as a series of clutches each season rather than as a single clutch.

Why should migrants be at a disadvantage in establishing themselves in new areas? As a broad generalization, the distribution of migrant species appears to reflect seasonal peaking of resources to levels beyond the capacity of resident species to exploit (Ashmole 1961, 1963; MacArthur 1959; Herrera 1978). If population sizes in resident species are limited by over-winter survival, very seasonal areas, with severe winters, will have rather low numbers of resident pairs breeding there each spring and considerable scope may remain for migrant individuals to invade the area seasonally for breeding. Because relatively few residents will survive each winter in very seasonal environments, those that do survive can be expected to sequester greater resources per head for their own breeding and therefore to breed more prolifically. As was first suggested by von Haartman (1968), the resident species enjoy the advantage of being on their breeding grounds from the start of suitable breeding conditions each year and so being able to start breeding as early as is physically possible, thus producing more young in total. Finally, since resident individuals that survive winter adversity do so by virtue of competitive ability, they can be expected to be intrinsically more competitive than migrants that have overwintered in more favourable and probably less competitive climates. These four points have been confirmed by empirical data. Herrera (1978) has used European census data to show that more seasonal areas support proportionately more migrant birds than do less seasonal regions. Secondly, clutch sizes are larger among residents in the more seasonally productive areas (Ricklefs 1980). Thirdly, migrants breed later the longer the migratory journey they undertake, with the most sedentary resident species enjoying the earliest start of breeding (O'Connor 1985). The more migratory species also suffer proportionately greater reduction in chick production for any given delay to their start of breeding (O'Connor 1985). Finally, there exists a marked interspecific gradient between the extent of migratory journey undertaken and the severity of density dependence in fledgling productivity (O'Connor 1985).

These various points combine to indicate that migrants are unlikely to be able to compete successfully with resident species, but does not actually demonstrate that such competition between the two groups actually occurs. For North American birds, Cox (1968) has shown that variation in culmen size is greater among resident groups than among migrant groups, a finding he interpreted as showing that migration evolved in groups that have been unable, or that have not been forced, to differentiate morphologically as a means of ecological isolation. A similar pattern is apparently present among European species; I have examined the extent to which habitat segregation and feeding segregation provide coexistence mechanisms among migrant and resident species by analysing the data of Lack (1971). Among resident species, habitat segregation accounts for just 24 % and food segregation for 14 % of the congeneric pairs considered; among migrant congeners, however, the corresponding proportions are 60 % and 9 % respectively. This result suggests that interspecific habitat competition may be far more significant for migrant species than it is for resident species. One might therefore expect migrants to be restricted in habitat competition with the hypothesized, more competitive, resident species. Examination of the spectrum of nesting habitats used by six resident and six migrant species in the 1963 summer, after the massive population reduction brought about among residents by the severe conditions of the 1962–63 winter, shows that five of the six resident species decreased the diversity of habitats in use (R. J. O'Connor, unpublished observations), as expected from habitat competition models (Brown 1969; Fretwell & Lucas 1969; see O'Connor (1985) for a recent review). In contrast, the migrant species, which escaped the winter by being in Africa and whose population changes between the two summers were relatively small, generally increased in range of habitats used; this observation suggests that they had previously been excluded from these habitats by competition from residents.

Cox (1968) has advanced a number of evolutionary processes by which migrant bird populations could have evolved to escape competition with resident species. If such models are valid, it is not surprising to find that migrant species are later unable to invade alien communities.

The role of source populations

The geographical location of successful and unsuccessful invasion sites in Britain suggests that locations closest to continental source populations from which further immigrants can be drawn, i.e. those in south-east England and in Scotland, are most successful. It is possible that ecological conditions in south-east England are different from those elsewhere in the country and that it is this, rather than the proximity of sources of further immigration, that favours colonists. Fuller (1982) and A. P. Dobson (unpublished) have shown that the numbers of species present in woodland bird communities decrease systematically along a gradient from southeast to northwest. This might reflect a similar trend in plant or invertebrate numbers or in overall productivity. However, a marked longitudinal cline in the number of species breeding on farmland, with greater numbers in the east, has also been established (O'Connor & Shrubb 1986), and clines in bird communities within this highly managed habitat (especially in eastern England, where intensive cereal cultivation is prominent) may be less likely to reflect clines in natural vegetation, although the possibility of a gradient in productivity remains. The possibility that the cline reflects accumulated colonizations of Britain by bird species invading from the European continent is an intriguing one. One might note that Scotland, the other area of successful colonizations (figure 3), has no fewer than 19 species that breed nowhere else in Britain (Thom 1986). This fact again raises the possibility (at the risk of over-interpreting the available evidence) that this species-richness is also the outcome of accumulated invasions, in this case from Scandinavia. It has been suggested that the decline of the wryneck, *Jynx torquilla*, in southern England concerns a possibly climate-induced retreat on the part of a southern population, while Scotland has been recolonized afresh by birds from the Fenno-

Scandinavian population (Sharrock 1976). Scotland does, however, offer rather different habitats from those found in England and Wales (Fuller 1982) and the similarity of these to habitat types in Scandinavia may also be relevant.

The role of reproductive rates

The results presented here show that successful invaders produce more eggs each season than do unsuccessful invaders. MacArthur & Wilson (1967) stressed the importance of high rates of population increase in escaping from the initial risk of random population extinction. Amongst the various resident species that suffered major mortality during the severe winter of 1962–63, those laying most eggs each season were the earliest to recover their pre-crash levels (O'Connor 1981). Population densities were otherwise largely influenced by density-dependent mechanisms (see, for example Batten 1977; O'Connor 1980, 1982). The ability to compensate for a large population fluctuation is thus one advantage to an invader of having a large reproductive capacity, particularly when in a competitive environment. However, even among less competitive migrant birds, egg production is correlated with range (O'Connor 1981), so invading species with high productivity may be able to spread more rapidly over many sites than they would if less productive, thereby reducing the risk that, for example, habitat destruction at a single founder site will eliminate the population before it can spread.

It is arguable that the achievement of high rates of population increase by the evolution of low death rates would be a safer strategy than doing so by high reproductive output (MacArthur 1972), but this is true only if the annual variance in mortality is also low. Where annual mortality is more or less constant, a fixed proportion of each season's reproductive output is needed to compensate for annual mortality. Where the same death rate is the outcome of exceptionally heavy mortality in a very few years but generally low mortality in most years, cumulative population growth will often distance the invader population from the region of stochastic extinction risk before a bad year is encountered. Only if a year of heavy mortality is experienced early on is there likely to be any advantage in achieving a high birth : death ratio through lower death rate than through high birth rates.

MacArthur & Wilson's (1967) model relates invasion persistence to the ratio of birth and death rates rather than to either alone. This raises an interesting area for investigation in relation to the trade-offs between reproductive effort and survival suggested by Cole (1954) and Stearns (1976). If higher reproductive rates are achievable only at the cost of an associated increase in mortality, ratios of birth rate to death rate ought to be less variable than is the case for natality or mortality alone. The evolution of a successful invasive strategy ought, therefore, to be more difficult to achieve than is apparent in considering demographic parameters in isolation. In practice, however, it may be that survival–reproduction trade-offs operate within some, but not other, ecological strategies, with, for example, single-clutch species affected but multiple-clutch species unaffected (O'Connor 1985). This idea does appear to have consequences for invasive success, for multi-brooded species were more frequent among successful invaders than among species failing to establish themselves (table 2). This effect is consistent with the MacArthur–Wilson model, given the postulated restriction of demographic trade-offs to single-brooded species, for the production of a given number of eggs over two or more clutches escapes the mortality penalty associated with the same total of eggs in a single clutch. The birth rate : death rate ratio of the MacArthur–Wilson model is therefore increased for multi-brooded species, promoting the likelihood of persistence in the face of chance fluctuations in population size. Other considerations may also favour producing several clutches, rather than one, for the same total egg production. In a high predation régime, for example, repeated laying of small clutches with a short nest cycle is a more productive strategy than is the laying of a very large clutch with a long nest cycle (Foster 1974). In an alien community, to which they are not well adapted, invaders may well find themselves subject to greater predation than in their native communities. The collared dove is interesting in this respect; it lays as many as five clutches of two eggs in a single season, but, as with most other doves (excluding hole-nesting species as the stock dove, *Columba oenas*), it is vulnerable to predation (Robertson 1984). Best & Stauffer (1980) have shown that species that occupy a wide range of nesting sites are more vulnerable to nest predation than are species with narrow ranges of sites, so it is interesting that the collared dove is thought by at least some British birdwatchers to have contracted in range of nesting habitats in recent years. The success of the Royal Society for the Protection of Birds in fostering, by special protection, the successful re-establishment of heavily persecuted species, such as the osprey, *Pandion haliaetus*, may well indicate that human predation is of importance in restricting the success of some invasive birds.

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APPENDIX 1. CLASSIFICATION OF SPECIES ANALYSED IN THE PAPER

(The status categories recognized are: N, native rare breeder; S, sporadic (occasional or intermittent) breeder; R, recolonist; I, invader. See text for details.)

species	status	species	status
great northern diver, *Gavia stellata*	S	green sandpiper, *Tringa ochropus*	S
Slavonian grebe, *Podiceps auritus*	I	wood sandpiper, *Tringa glareola*	I
red-necked grebe, *Podiceps grisegena*	S	spotted sandpiper, *Actitis macularia*	S
black-necked grebe, *Podiceps nigricollis*	I	turnstone, *Arenaria interpres*	S
bittern, *Botaurus stellaris*	R	Mediterranean gull, *Larus melanocephalus*	I
little bittern, *Ixobrychus minutus*	S	little gull, *Larus minutus*	S
whooper swan, *Cygnus cygnus*	S	gull-billed tern, *Gelochelidon nilotica*	S
pintail, *Anas acuta*	I	black tern, *Chlidonias niger*	S
garganey, *Anas querquedula*	N	collared dove, *Streptopelia decaocto*	I
tufted duck, *Aythya fuligula*	I	snowy owl, *Nyctea scandiaca*	S
scaup, *Aythya marila*	S	bee-eater, *Merops apiaster*	S
long-tailed duck, *Clangula hyemalis*	S	hoopoe, *Upipa epops*	S
common scoter, *Melanitta nigra*	I	wryneck, *Jynx torquilla*	I
goldeneye, *Bucephala clangula*	I	shore lark, *Eremophila alpestris*	S
goosander, *Mergus merganser*	I	bluethroat, *Luscinia svecica*	S
honey buzzard, *Pernis apivorous*	N	black redstart, *Phoenicurus ochruros*	I
red kite, *Milvus milvus*	N	fieldfare, *Tardus pilaris*	I
marsh harrier, *Circus aeruginosus*	R	redwing, *Turdus iliacus*	I
Montagu's harrier, *Circus pygargus*	N	Cetti's warbler, *Cettia cetti*	I
osprey, *Pandion haliaetus*	R	Savi's warbler, *Locustella luscinioides*	R
hobby, *Falco subbuteo*	N	marsh warbler, *Acrocephalus palustris*	N
Pallas' sandgrouse, *Syrrhaptes paradoxus*	S	moustached warbler, *Lusciniola melanopogon*	S
spotted crake, *Porzana porzana*	R	icterine warbler, *Hippolais icterina*	S
Baillon's crake, *Porzana pusilla*	S	Dartford warbler, *Sylvia undata*	N
avocet, *Recurvirostra avosetta*	R	firecrest, *Regulus regulus*	I
red-necked phalarope, *Phalaropus lobatus*	N	golden oriole, *Oriolus oriolus*	I
stone curlew, *Burhinus oedicnemus*	N	red-backed shrike, *Lanius collurio*	N
little ringed plover, *Charadrius dubius*	I	serin, *Serinus canaria*	I
Kentish plover, *Charadrius alexandrinus*	S	brambling, *Fringilla montifringilla*	S

Appendix 1 (*cont.*)

species	status	species	status
dotterel, *Charadrius morinellus*	N	scarlet rosefinch, *Carpodacus erythrinus*	S
black-winged stilt, *Himantopus himantopus*	S	parrot crossbill, *Loxia pytopsittacus*	S
Temminck's stilt, *Calidris temminckii*	I	Lapland bunting, *Calcarius lapponicus*	S
purple sandpiper, *Calidris maritima*	I	snow bunting, *Plectrophenax nivalis*	I
ruff, *Philomachus pugnax*	R	cirl bunting, *Emberiza cirlus*	N
black-tailed godwit, *Limosa limosa*	R		

Discussion

M. B. Usher (*Department of Biology, University of York, York YO1 5DD, U.K.*). In his paper, Dr O'Connor has elegantly shown that invasibility is not related to migration. However, movement in birds is of two broad types: migration and dispersal. The latter is probably most important after fledging of the young. Does he have any informtion on ranges of dispersal, and whether this factor is related to invasibility?

R. J. O'Connor. Some anecdotal evidence exists as to birds of the year turning up in the 'wrong' places in late summer or during autumn migration, but the influence of juvenile dispersal on invasibility has not been studied. Dispersal range appears to vary between species and even between sexes within a species and for at least some species may vary with the density of the population into which the young birds are born. To this extent, therefore, the question can be subsumed in the discussion of these matters. Whether extensive juvenile dispersal contributes separately to the likelihood of successful invasion (for example, by spreading juveniles of a colonizing propagule into new sites away from the founder one and thus reducing the sensitivity of the population to site-related changes) is nevertheless an interesting question.

A. Gibbs (*Research School of Biological Sciences, Australian National University, P.O. Box* 475, *Canberra, A.C.T.* 2601, *Australia*). There are two kinds of bird: regular migrants and chance migrants. In the recent meeting on the SCOPE programme in Australia, H. Nix of CSIRO showed that the strength of colonization by chance migrants is correlated with the climatic similarity of their area of origin and their new territory. He calculated this similarity from 16 weather parameters and called it a 'bioclimatic index'.

R. J. O'Connor. I use 'migratory' in my paper to mean long-distance migrants that breed regularly in one area but winter in another, such as the swallows that breed in Britain and winter in Africa. It may be argued that such species should be best able to colonize new areas but this appears not to be the case; instead, they move out seasonally.

The occurrence of migrant individuals within bird communities has been shown by Herrera (1978) to be correlated with climatic seasonality. Migrants are essentially exploiting a seasonal increase in food supplies that is beyond the capacity of resident species, limited by winter severity, to exploit. Migrants can therefore move into and breed in areas with very seasonal climates, more so than they can with less seasonal climates. In a very seasonal country, such as Finland, those birds that can overwinter start with an advantage in exploiting seasonally available food, by virtue of being on site from the start, but they cannot take it all, thus leaving an opening for summer migrants. Such dynamics mean that any invader becoming a resident in Finland must be pre-adapted to severe climates, i.e. successful colonists are likely to come from areas of similar climate; however, in like manner, any colonizing migrants, geared to exploiting very seasonal foods for breeding, are likely to share climatic conditions of origin.

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K. C. Brown (*Department of Biology, University of York, York YO1 5DD, U.K.*). Has anyone compared the genetics of collared doves in Britain and eastern Europe? Do we know whether they are the same?

R. J. O'Connor. I am not aware of any studies of this kind.