Biol Invasions (2008) 10:659–672
DOI 10.1007/s10530-007-9160-7

ORIGINAL PAPER

Non-indigenous terrestrial vertebrates in Israel and adjacent areas

Uri Roll · Tamar Dayan · Daniel Simberloff

Received: 29 July 2007 / Accepted: 10 August 2007 / Published online: 5 September 2007

Abstract We investigated characteristics of established non-indigenous (ENI) terrestrial vertebrates in Israel and adjacent areas, as well as attributes of areas they occupy. Eighteen non-indigenous birds have established populations in this region since 1850. A database of their attributes was compiled, analyzed, and compared to works from elsewhere. Most ENI bird species are established locally; a few are spreading or widespread. There has been a recent large increase in establishment. All ENI birds are of tropical origin, mostly from the Ethiopian and Oriental regions; the main families are Sturnidae, Psittacidae, Anatidae, and Columbidae. Most species have been deliberately brought to Israel in captivity and subsequently released or escaped. Most of these birds are commensal with humans to some degree, are not typically migratory, and have mean body mass larger than that of the entire order. ENI birds are not distributed randomly. There are centers in the Tel-Aviv area and along the Rift Valley, which is also a corridor of spread. Positive correlations were found between ENI bird richness and mean annual temperature and urbanization. Mediterranean forests and desert regions have fewer ENI species than expected. Apart from birds we report on non-indigenous species of reptiles (2) and mammals (2) in this region.

Keywords Birds · Introduced species · Israel · Land vertebrates · Non-indigenous species

U. Roll (✉) · T. Dayan
Department of Zoology, Tel Aviv University,
Tel Aviv 69978, Israel
e-mail: uroll@post.tau.ac.il

D. Simberloff
Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville,
TN 37996-1610, USA

Introduction

Non-indigenous species are thought to be the second most destructive human influence on biodiversity (Schmitz and Simberloff 1997; Walker and Steffen 1997), affecting local environments (Simberloff 1996; Parker et al. 1999) and also threatening agriculture (Mack et al. 2000; Pimentel et al. 2000). Non-indigenous land vertebrates have been noted and studied in many locations (e.g., Long 1981, 2003; Lever 1985, 1987, 2003). Impacts of many species have been widely described, and there have been several attempts at regional or global syntheses (e.g., Ebenhard 1987). Various attributes of their establishment success or lack thereof have been investigated (Jeschke and Strayer 2005). Despite this literature, data are still lacking on the generality of observed patterns, and for most regions there is no comprehensive treatment of non-indigenous land vertebrates.

Here we examine established non-indigenous (ENI) terrestrial vertebrates in Israel and the surrounding area. The southern Levant is where the Eurasian and African land masses meet and has been a land bridge for both animals and humans and their goods for many millennia (Tchernov 1988). We therefore expect it to have many non-indigenous species. However to date, no comprehensive work has addressed the ENI land vertebrates of this region. We determine various attributes of ENI species in this region and compare them to information from elsewhere. We also investigate these species with respect to various spatial attributes as well as their spread between different sub-regions.

Methods

We studied ENI land vertebrates of Israel, the Golan Heights, the West Bank, and Gaza Strip, an area of about 27,500 km^2 (see also Yom-Tov 1988). The scope of this work is all land vertebrates of this region. However, there are few non-indigenous reptiles and mammals, and probably no ENI amphibians. Therefore, most analyses are of ENI birds. Birds included were only those known to reproduce in the wild. However, we excluded migrating birds that usually pass over this region or overwinter in it and have recently begun to nest here. Also excluded were birds that increased their range within the boundaries of Israel and adjacent areas owing to human actions; these have been analyzed elsewhere (Mendelssohn and Yom-Tov 1999b; Hatzofe and Yom-Tov 2002).

We used several sources of information: scientific and gray literature for both local species and as worldwide references, experts' overview of this phenomenon in this region, specific data from the Tel Aviv University natural history collections, and several internet-based databases, mainly for general data on local species. For each species we recorded systematic affinity, life-history attributes, food habits, range of native population, range of source population for this introduction, new geographic range in this region, history of spread in this region and in the world, local dispersal methods, means of introduction to this region, ecosystems invaded, year of first discovery in this region, economic or environmental impact (in this region), records of introduction elsewhere, and status of the species in this region.

Spatial patterns of ENI birds were based on their distribution in the 29 different bird regions of Israel and its adjacent areas (Shirihai 1996) and were analyzed using ESRI—ArcView GIS 8.2 software. We compared the basal occurrence layer, highlighting hotspots of ENI birds, to various data layers, including mean annual temperature, mean annual precipitation, vegetation types, intercity roads and their margins, layout of human settlements, and occurrence of nature reserves and national parks. We also compared occurrence of ENI bird species to that of native resident birds and of native land vertebrates in general, in 30*30 km quadrats. The basal ENI species region layer was given new sets of values for temperature, precipitation etc. We then calculated correlations between ENI species richness and the various attributes. We checked for autocorrelation between the various spatial correlates. Later we conducted backwards stepwise multiple regressions between the spatial correlates and ENI bird species richness in the different regions.

We also compared bird spatial patterns to the distribution of 34 recognized vegetation types of Israel (Zohary 1982). To estimate the number of ENI bird species in the vegetation types, we overlaid the map of the 34 vegetation types on that of the 29 bird regions, dividing Israel into many smaller polygons, each consisting of part of a bird region and a vegetation type. The number of species in each vegetation type was calculated as the weighted average of the number of ENI bird species in each of its component areas. We later lumped and compared these vegetation types.

In the vegetation type analysis and the calculation of average native vertebrate and bird species richness in each invasive bird zone, we used a power function species–area relationship to estimate species numbers in the different new polygons. We used $z = 0.26$ in calculations because such a relationship approximates many literature examples (Whittaker 1998).

Results

Non-indigenous reptiles

Two introduced reptile species have been noted in wild habitats of Israel. The red-eared slider (*Trachemys scripta*) has been found since the mid-1970s (Bouskila 1986), but it is not known if it reproduces in the wild (Bouskila 2002). Its importation has been prohibited, but it is still smuggled. The rough-tail gecko (*Cyrtopodion scabrum*) was first discovered in 1989 and reproduces in the wild (A. Bouskila, personal communication).

Non-indigenous mammals

Currently two mammal species are considered ENI in this region. The nutria (*Myocastor coypu*) was introduced in the early 1950s from Chile (Bodenheimer 1958; Mendelssohn and Yom-Tov 1999a) and spread to most freshwater habitats in the Mediterranean region of Israel, even polluted ones. A recent introduction is the Indian palm squirrel (*Funambulus pennati*), found near Mitzpe Ramon in the Negev. Little is known about this introduction; several eradication attempts have failed.

Non-indigenous birds

Twenty-five bird species were included in the database. However, seven were classified as either misidentification or "introduced" (birds not reproducing in the wild); this last group is thought to include many more species than those listed in the database. Only the 18 birds known to have established populations in nature were further analyzed. These ENI birds were divided into three status groups in accordance with Williamson (1996) (Table 1).

- Non-indigenous birds established locally and definitely reproducing in nature (14 species).
- Non-indigenous birds currently increasing in number and spreading to new localities (two species).
- Non-indigenous birds established in a widespread area but no longer significantly increasing numbers or range (two species).

The two widespread species are the laughing dove (*Streptopelia senegalensis*) and the Indian silverbill (*Lonchura malabarica*). The dove was introduced in the middle of 19th century by the Ottomans, to mosques, and spread mainly in old towns. From the early 20th century to the 1970s it spread to many new settlements of Israel (Paz 1986; Shirihai 1996) and is today widespread in all regions. It breeds year round (Shoham et al. 1997), and its population is several hundred thousand (Shirihai 1996). The Indian silverbill reached Israel in the 1980s and spread along the Rift Valley from Eilat to the Sea of Galilee. After its initial expansion during the 1980s it became an uncommon local breeder (Shirihai 1996).

The two species currently spreading are the rose-ringed parakeet (*Psittacula krameri*) and the common myna (*Acridotheres tristis*). The rose-ringed parakeet either reached Israel on its own or, more likely, escaped from captivity during the 1960s. Its first breeding was recorded in 1983 (Dvir 1985, 1988), and since then in it has spread to most regions of the country. The common myna was introduced in the late 20th century. Since 1998 it is increasing in numbers and range from the central coastal plain north, east, and south (U. Roll, pers. obs.).

The species currently established in small regions comprise several groups. The majority are escaped birds established in limited numbers in the central coastal plain, most notably in the Yarqon Park in Tel-Aviv. These include several starlings, parrots, ducks, and a weaver. Other introduced birds breeding locally are several passerines, the namaqua dove (*Oena capensis*), and the alexandrine parakeet (*Psittacula eupatria*); these are established in several locations along the Rift Valley from Eilat to the Bet-Shean Valley (or even further north). Most of these species are limited in numbers but a few are clearly increasing in numbers and range, although they have not yet dispersed to new regions (U. Roll, pers. obs.). Among these birds is the monk parakeet (*Myiopsitta monachus*), numbering several hundred individuals in the Yarqon Park in Tel-Aviv (Hatzofe and Yom-Tov 2002). The house crow (*Corvus splendens*) has been seen in Eilat since the mid-1970s and has bred there since 1979. Recent attempts to control this population have proved relatively effective (Nemtzov and Hatzofe 2003). The black-headed conure (*Nandayus nenday*) was spotted in 1970 in the Emeq-Hefer region and has bred there since 1993 (Beer 1994).

Systematic relations and biogeographic origins

The ENI birds come from four orders and seven families (Table 2). All are tropical: Ethiopian (7), Oriental (7), Neotropical (3), and Paleotropical (1).

Table 1 ENI bird species list, status codes, and known effects

Species name	Status code	Effects in this region	Effects worldwide
Acridotheres tristis	s	n (s)	p, n (r)
Alopochen aegyptiacus	el		p, n (s)
Amandava amandava	el		p (r)
Anas bahamensis	el		
Cercotrichas podobe	el		
Corvus splendens	el		p, n (r)
Lamprotornis sp.	el		
Lamprotornis superbus	el		
Lonchura malabarica	ew		
Myiopsitta monachus	el		p (r)
Nandayus nenday	el		p (r)
Oena capensis	el		
Ploceus velatus	el		p (r)
Psittacula eupatria	el		p (r)
Psittacula krameri	s	p (r), n (s)	p (r)
Streptopelia senegalensis	ew		p (r)
Sturnus burmannicus	el		
Sturnus nigricollus	el	n (s)	

Status codes: el—established locally, ew—established and widespread, s—spreading (see text for details). Effects codes: p—pest of agriculture or other practices, n—inflicts damage to native species, suspected damage (s), researched and shown to inflict damage (r)

Table 2 The number of ENI bird species from different orders and families. The number of native species from these families is also shown, after Shirihai (1996)

Order	Family	Invasive birds	Native birds
Anseriformes	Anatidae	2	33
Columbiformes	Columbidae	2	7
Psittaciformes	Psittacidae	4	0
Passeriformes	Corvidae	1	10
	Estrildidae	2	0
	Ploceidae	1	0
	Sturnidae	5	3
	Turdidae	1	38
Passeriformes total		10	
Total		18	

The nutria is originally from South America, The Indian palm squirrel is of Oriental origin. The red-eared slider is native from southern USA to Brazil, while the rough-tail gecko comes from other parts of the Middle East.

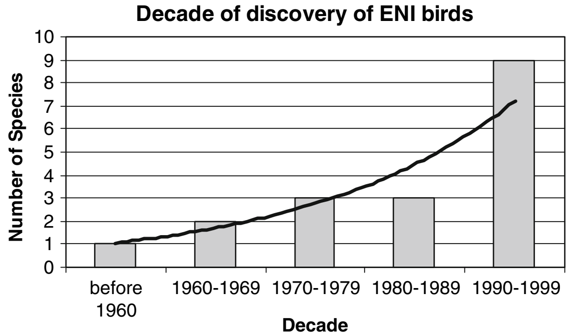

Fig. 1 Number of ENI birds first seen in each decade (included is an exponential trend line based on the data points)

Year of discovery

The ENI birds were categorized by decade of first appearance in Israel (see Fig. 1). Nutria were brought in the 1950s; the Indian palm squirrel has been found in wild habitats only in the past few years. The red-eared slider was first introduced in the early 1980s and the rough-tail gecko in the late 1980s.

Establishment pathways

Eleven of 18 ENI bird species are escaped cage birds (in some cases they may have also been released intentionally). Four other species arrived on their own but with human assistance. The Indian silverbill was most likely released from captivity elsewhere in the Arabian Peninsula and expanded its range to Israel and adjacent areas (later joined by escaped birds from Israel). The house crow accompanied ships along the Red Sea and the Gulf of Eilat (perhaps transported intentionally) and eventually established in Eilat and spread northwards. The namaqua dove and the black bush robin (*Cercotrichas podobe*) probably reached Israel by natural range expansion from Arabia. However, the expansion of these two Ethiopian birds into Arabia was presumably due to changing agricultural practices, so these two species were included as ENI. The pathway of introduction for three other species is unknown; they are presumed to be escapees (Nemtzov and Hatzofe 2003).

Nutria were brought intentionally for use in fur farms and as herbivores in aquaculture. The Indian palm squirrels are escaped pets. The red-eared slider was brought as a pet and probably escaped or was released into natural habitats. The rough-tail gecko was probably introduced unintentionally with cargo.

Human commensalisms and impact on agriculture and the environment

Of the 18 ENI birds, 14 are commensal with humans to some degree. Seven use urbanized habitats frequently, and seven others use either human habitats less frequently, or other anthropogenic environments such as agricultural fields, orchards, etc.

Eight ENI bird species are agricultural pests elsewhere and four others damage both agriculture and the native environment (Table 1).

In Israel two species (common myna and house crow) have been spotted harassing, preying on, or competing with local species of reptiles and birds. The rose-ringed parakeet is already considered an agricultural pest (Moran 2003) and is also thought to affect local hole-breeding bird species (Shirihai 1996). Several of these ENI species (starlings and parrots) are intelligent and aggressive (Sol et al. 2002), and further effects on the local fauna may be expected. Nutria are known in Israel to damage native plants of conservation concern and agricultural produce (Shalmon 1999; Moran 2003). The red-eared slider is feared to compete with local turtle species (Ilani 1985; Motro 2001). The rough-tail gecko is not known to harm local species in Israel. However, for none of these species has there been a direct demonstration of population impact.

Natural history attributes of established non-indigenous birds

Half (nine species) of the ENI birds are sedentary. Six other species are partially nomadic—they either have a few migratory populations or exhibit some migratory behavior at the edge of their native range. For three other species, migratory behavior is unknown. No ENI bird is truly migrant. There was no distinguishable pattern at the family level of belonging to one migratory category or the other.

The mean body mass of ENI birds in Israel is 96.2 g (median 110 g), almost twice the mean body mass of over 6,000 birds worldwide, 53.2 g (median 37.06) (Blackburn and Gaston 1994; Maurer 1998).

Table 3 Number of ENI birds feeding on each food type (17 species)

Nutrition (cumulative)	Number of species using this food type
Seeds or grain	14
Insects	10
Fruits	9
Grass, leaves, or flowers	8
Nectar	3
Invertebrates other than insects	2
Human refuse	2
Birds	1

We tabulated food preferences and habitats of the ENI birds in their native ranges, where possible (Table 3); in many cases a single species was assigned to more than one category. With respect to native habitat use, seven occupy forest habitats, five arid habitats, three aquatic habitats, one open grassland habitats, and two varied habitats.

Israeli range of non-indigenous vertebrates

The ranges and number of ENI birds species were plotted on a map of Israel divided into 29 regions (Shirihai 1996). Figure 2 shows the number of species in each region.

Nutria are found throughout the Mediterranean region of Israel, in various aquatic habitats. The Indian palm squirrel is found only near Mitzpe Ramon in the Negev Desert. The rough-tail gecko is found near the city of Eilat. The red-eared slider is found in several freshwater habitats in the central part of Israel.

Spatial analysis of established non-indigenous birds

There is no significant correlation between the number of ENI bird species in a region and its area (Pearson correlation; $r = -0.144$; $r^2 = 0.02$; $P = 0.455$).

We compared several spatial features to the number of ENI bird species in the 29 different regions (Table 4). The number of invasive species is significantly correlated only with mean annual temperature (Pearson correlation; $r = 0.444$; $r^2 = 0.197$; $P = 0.0158$). Mean annual temperature is negatively

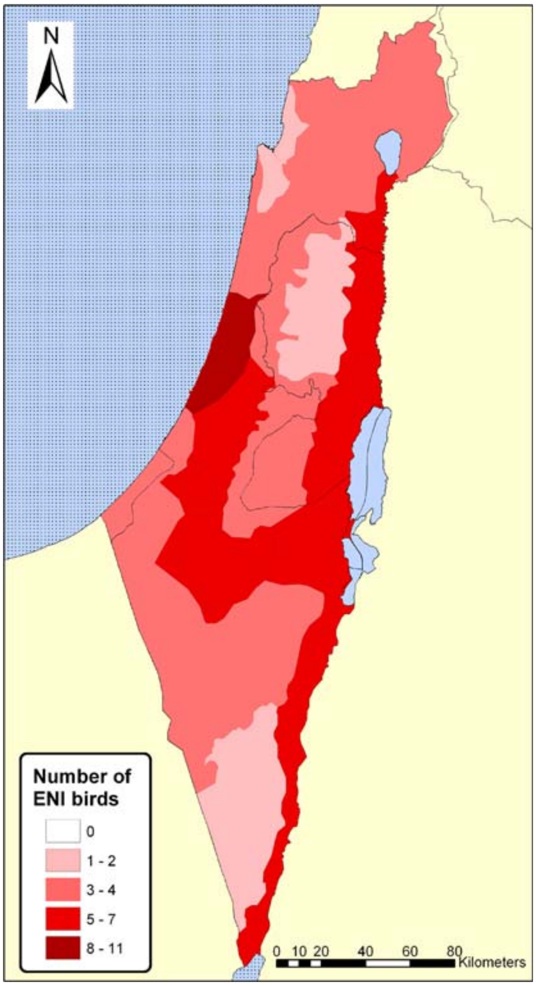

Fig. 2 Number of ENI bird species in the different regions of Israel and adjacent areas (Cassini Soldner projection)

correlated with the number of native vertebrate species and mean annual rainfall and positively correlated with reserve area proportion, road-free areas, and settlement-free areas, but none of these variables is correlated with number of ENI bird species. By backwards stepwise multiple regression, we compared all the different spatial attributes to the number of ENI bird species in each region. Again only mean annual temperature remained significant ($r = 0.444$; adjusted $r^2 = 0.167$; $P = 0.0158$).

We estimated ENI bird richness (excluding the Golan Heights and Mt. Hermon) as described above for the 34 vegetation zones (Zohary 1982). Appendix 1 lists zones and estimated numbers of ENI species. We lumped these vegetation types into six major vegetation and soil types (see Appendix 1 for the lumping principle) and also estimated total average species number for these six types (Fig. 3). Of the six major vegetation and soil types, Mediterranean plains and coastal and internal sands had the most ENI birds, while Mediterranean forests and maquis had the fewest.

Spread of non-indigenous land vertebrates over this region

ENI birds show two distinct patterns of spread. The first is a spread north, east, and south from the Dan (Tel-Aviv) region (e.g., rose-ringed parakeet, common myna). The second spread pattern is northwards along the Rift Valley from Eilat or the southern Arava up to the Jordan valley and in some cases even as far north as the Golan Heights and Upper Galilee (e.g., red waxbill—*Amandava amandava*, namaqua dove, Indian silverbill). The house crow spread northwards from Eilat only as far as the southern Arava.

The rough-tail gecko also displays this pattern of spread from its initial appearance in Eilat northwards along the Rift Valley, as well as southwards into the Sinai Peninsula (Amitai and Bouskila 2001).

Nutria spread from several localities in northern Israel southwards to most freshwater habitats (both natural and artificial) in the Mediterranean region of Israel and have also been found in several localities in Jordan (Bodenheimer 1958; Qumsiyeh 1996; Mendelssohn and Yom-Tov 1999a).

Introduction elsewhere of non-indigenous land vertebrates of this region

Eleven of the ENI bird species have been noted as non-indigenous elsewhere (Table 5). Some of these species (e.g., the common myna, rose-ringed parakeet, monk parakeet, and others) have been found to be problematic elsewhere (Long 1981; Lever 1987). Nutria have been introduced to many places and in most are considered a pest (Carter and Leonard 2002). The red-eared slider is also notoriously invasive in Asia, the Middle East, Europe, and other regions (Luiselli et al. 1997; Cadi and Joly 2003). The rough-tail gecko was introduced to Texas with negative effects on a different introduced gecko (the house gecko, *Hemidactylus turcicus*, which is native

Table 4 Matrix of correlations (upper triangle) and associated probabilities (lower triangle) among all candidate independent variables plus number of ENI species, over the 29 regions (correlations significant at the 0.05 level are underlined)

Correlation r / P- value	Num. of ENI birds	Native bird proportions	Average vertebrates proportions	Average annual temperature	Average annual rainfall	Reserve area proportion	Road free area / total area	Settlement free area / total
Num. of ENI birds		0.0708	-0.0099	0.4440	-0.2026	0.0086	-0.0380	0.0254
Native bird proportions	0.7151		0.8230	-0.2310	0.3371	-0.0637	-0.0397	-0.0497
Average vertebrates proportions	0.9595	4.24E-08		-0.4012	0.2367	-0.2146	-0.0088	0.0342
Average annual temperature	0.0158	0.2279	0.0310		-0.7183	0.4453	0.4150	0.5024
Average annual rainfall	0.2919	0.0738	0.2163	1.15E-05		-0.5826	-0.7228	-0.8680
Reserve area proportion	0.9647	0.7429	0.2636	0.0155	9.13E-04		0.6246	0.6765
Road free area / total area	0.8447	0.8378	0.9639	0.0252	9.49E-06	2.92E-04		0.8623
Settlement free area / total	0.8958	0.7981	0.8604	0.0055	1.07E-09	5.60E-05	1.83E-09	

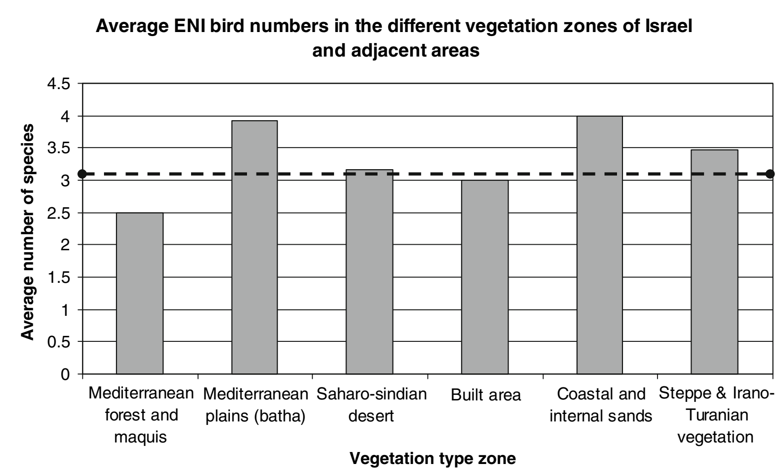

Fig. 3 Average ENI bird species numbers for different vegetation zones in Israel and adjacent areas. Dashed line shows the overall average species number for all zones

to Israel and adjacent areas) (Klawinski et al. 1994; Vaughan et al. 1996).

Discussion

Two main questions underlie invasion biology research: what makes a good invader and what determines invasibility of a specific habitat (Lodge 1993)? Some claim that several distinct features of both species and habitats can be discerned, while others argue that few generalizations are firm (Moulton and Sanderson 1997, 1999; Duncan and Young 1999; Kolar and Lodge 2001a, b; Rejmanek and Reichard 2001; Sol 2001). Several patterns of the

Table 5 Regions invaded by Israeli ENI birds. Numbers for each region represent how many species (out of a total of 11) are found in this region

Invaded region	Number of birds
Middle east	8
Pacific islands	5
Europe	4
Atlantic islands	4
Nearctic	3
Australia	2
Indian ocean islands	2
Ethiopian	2
Neotropic	1
Oriental	1

non-indigenous land vertebrates of this region bear on these questions.

Most of the ENI vertebrates were introduced only in the past two decades. This is perhaps due to the great intensification of trade and the shortened travel times together with the increased standard of living (Yom-Tov 1988). Israel has no long history of bird introductions, acclimatization societies or an extensive culture of hunting fowl. Consequently, Israel and adjacent areas have no extensive record of bird introductions. Also, no vertebrates were introduced to this region for biological control.

Year of introduction (Fig. 1) shows a sharp increase in the number of ENI birds since the 1990s (half of all ENI bird species were introduced since 1990) that is due to the release of many bird species from a bird zoo in Tel Aviv. Many birds held in improper containment facilities escaped to a nearby city park, and from there to other parts of this region. This fact biases many analyses, because it accounts for the establishment of many (possibly 8 of 18 species) of the birds in this database. It could be that birds chosen for display in the facility, those that by chance had improper cages or were able to sustain themselves in the nearby park, skew the data and analyses. Nevertheless, some interesting observations are possible.

Biogeographical origin

All ENI birds in this region are tropical. This contrasts with the representation of introduced tropical species in most locations, except for Hawaii (Long 1981; Blackburn and Duncan 2001a); "although there has been no formal test, species from tropical regions appear to be greatly under-represented in lists of introduced species" (Duncan et al. 2003).

Unlike birds, the other non-indigenous land vertebrates are not necessarily tropical in origin. Also, ENI insects and fishes have arrived from both tropical and temperate regions (Roll et al. 2007a, b). Our bird data also conflict with the "climate/environmental matching" hypothesis (Duncan et al. 2003)—that introduced species will most likely succeed in locations within their native biogeographical region because they will face similar environments to those in their native range (Blackburn and Duncan 2001b; Cassey 2003).

The predominantly tropical origin for the region's non-indigenous avifauna could reflect our definition of non-indigenous species, or it could represent a true advantage that tropical ENI birds have in this region. This study included only birds that were *added* to the Israeli checklist in the second half of the 20th century (except for the laughing Dove). Hence, migrating birds that pass over this region or even winter in it, and began breeding—for example, the great cormorant, *Phalacrocorax carbo* (Hatzofe and Yom-Tov 2002)—were not included. Many temperate bird species migrate over Israel annually (Leshem and Yom-Tov 1996), but their establishment would not appear in the data. A few of the over 300 species not resident in this region but part of the Israeli checklist (Shirihai 1996) did find changing conditions in Israel favorable for reproduction and establishment. However, most did not do so for several millennia despite traversing this region once or twice a year. Migration over Israel may have already "selected" those Palearctic birds suitable for establishment. This could also be true for wandering birds traversing this region. Therefore they could not be non-indigenous by definition—they would not be regarded as such if they changed their status in the Israeli checklist (for example from a vagrant to a resident bird). This mechanism could not play such a role for tropical birds that do not migrate over this region.

By contrast, the pattern could reflect an advantage of tropical birds in any stage leading to establishment. Tropical birds are over-represented, as opposed to Palearctic ones, in importation permits (S. Nemtzov, pers. comm.). Birders sometimes release tropical birds because they are beautiful and people want to see them (R. Elazari-Volcani, pers. comm.). But apart from higher introduction probabilities, tropical birds may also have an easier time establishing in Israel. Most resident Israeli birds are of Palearctic origin (Yom-Tov 1988), and perhaps there are more available niches, less competition, or fewer natural enemies for arriving tropical, birds. It is also possible that gardening and agricultural practices have created many more "pseudo-tropical" habitats for tropical birds (see below).

Taxonomic affiliation of the invasive birds

ENI birds include a few from families that have not been part of the regional avifauna—parrots, weavers, and waxbills (Psittacidae, Ploceidae, and Estrildidae, respectively) (see Table 2). Five of the 18 species of ENI birds are starlings (Sturnidae). In data compilations from many regions this family was not noted as one more likely to be successfully introduced (Lockwood 1999; Blackburn and Duncan 2001a).

Invasion pathways

Eleven of the ENI species of Israel are escaped cage birds, and a further three are presumed escapees. Israel did not have intentional bird introductions (except for perhaps the laughing dove). Two species (namaqua dove and black bush robin) reached Israel by what could be regarded as natural range expansion. Nevertheless they were included as ENI species because it is thought that changing human practices in the Arabian Peninsula enabled their arrival in Israel (Shirihai 1996). Their ENI status is also reflected by recent observations of range and abundance increase in Israel at least for the namaqua dove.

The red-eared slider is also a pet that escapes or is intentionally released. Importation of this species into Israel is prohibited, but it is probably still present in pet stores and zoos. It may also be smuggled.

Life-history attributes of the invasive birds

In many studies, various life-history attributes have been correlated with introduction success in birds (but see Simberloff 1986; Kolar and Lodge 2001a; Cassey et al. 2004; Colautti et al. 2006). We investigated some of these attributes in the birds that invaded this region. In accord with findings from elsewhere (Veltman et al. 1996; Sol and Lefebvre 2000), all ENI birds in this region are not migratory and most are entirely sedentary.

The mean body mass of ENI birds in this region is almost twice that of the average for over 6,000 birds (Blackburn and Gaston 1994; Maurer 1998) and is similar to the mean of 116.6 g for introduced birds elsewhere (Cassey 2001).

Local range and spread of the non-indigenous vertebrates

Two hotspots of ENI birds are the Dan region in the central coastal plain and in and around the city of Tel Aviv (Fig. 2). These could result from the fact that they are the most heavily populated region of Israel and encompass more disturbed habitats or opportunities for entry. This region also has high densities of ENI insect species (Roll et al. 2007a). But the avian pattern might be an artifact of releases from a bird zoo (see above). The Dan region is also a starting point for spread of ENI birds to other regions.

Other areas with many ENIs are the southern plains and northern Negev, but a distinct region, the Rift Valley (from Eilat in the south to the Sea of Galilee in the north), contains many ENI birds. This is also where the rough-tailed gecko is found.

There are several possible explanations for this pattern.

(1) Eilat, at the southern tip of this elongated basin, is a port of entry for goods of tropical origin. Birds may accompany humans and their goods from this port and spread northwards. For the house crow, this mode of introduction is suspected in both Israel (Shirihai 1996; Hatzofe and Yom-Tov 2002) and other countries along the Red Sea (Long 1981; Lever 1987; Shirihai 1996). The rough-tailed gecko also displays this pattern (Amitai and Bouskila 2001).

(2) The Jordan and Arava Valleys constitute the longest land border of this region with the Hashemite Kingdom of Jordan (335 km long). Birds introduced into countries to the east, and

spreading, will reach Israel and adjacent areas first in the Rift Valley. Further west lie the central mountain ridges of the Galilee, Samaria, Judea, and the Negev mountain ranges that may, to some extent, bar expansion. An example of such a secondary expansion from Jordan is that of the Indian silverbill, which has presumably escaped from captivity in various countries in the Arabian Peninsula and entered Israel from several localities along the Jordanian border (Shirihai 1996).

(3) The Arava and Jordan Valleys may provide suitable habitat for many tropical birds. The Rift Valley boasts a desert or semi-desert climate with hot and dry summers and warm, nearly rainless winters (Jaffe 1988). Human settlements and activity in these regions have greatly increased availability of freshwater and food for wildlife (Mendelssohn and Yom-Tov 1999b), thus creating new pseudo-tropical conditions along the Rift Valley. This change could have aided establishment of such species as the black bush-robin, namaqua dove and red waxbill.

Spatial correlates of established non-indigenous birds

The mean numbers of ENI bird species in the various locations are positively correlated with mean annual temperature, $r^2 = 0.197$. This result could imply that ENI birds, all of tropical origin, find warmer regions favorable for establishment (see above). Mean annual temperature correlated with other spatial predictors (see Table 4), but none proved significant by itself or contributed to the multiple regression model. The Dan region holds the most ENI bird species (11 of 18) and is the most heavily populated region of Israel and adjacent areas. However, no spatial correlate in our analysis that is linked with human disturbances (such as presence of settlements or roads) correlates significantly with ENI bird species numbers. This lack of correlation can be explained in two ways. First, the spatial analysis is crude and better point data on bird localities might improve predictions (unfortunately such data for all of the species are missing). It is also possible that the Dan region is an outlier in the data that is masked by other regions. The ENI birds in this region are predominantly found near human dwellings, agricultural fields and anthropogenic environments.

Vegetation zones

The number of ENI species from the different vegetation zones does not necessarily reflect the relative attractiveness of these zones to non-indigenous species (see Appendix 1, Fig. 3), because the different zones do not necessarily contain their natural vegetation (owing to human activities). The coastal and internal sands and Mediterranean Batha (low grasslands) have high average numbers of ENI bird species. These original vegetation types/topsoil covers in the coastal plain of Israel have been greatly altered by humans. These are the most anthropogenically disturbed habitats in this region (Dolev and Perevolotsky 2002), which could explain their high numbers of ENIs.

ENI bird species need not use the same habitats in the introduced and native ranges. Whereas the two habitat types used by most ENI birds in their native ranges are forest and arid habitats, these two vegetation zones—Mediterranean woodlands and Saharo-Sindian vegetation—hold fewer than the average number of species (Fig. 3).

Introduction of the non-indigenous vertebrates elsewhere and their control

Eight of the region's ENI birds are found in other Middle Eastern countries. This number could be an underestimate, because Israel's neighboring countries lack extensive faunal surveys. Some of the region's ENI birds are notorious in many parts of the world, (Table 5). These species were undoubtedly already invasive in many localities before their entrance into this region; however, they were admitted and in some cases (e.g., the common myna) their spread could have been nipped in the bud but was not. In general, control measures of ENI birds in this region are few.

Both the nutria and the red-eared slider are named among the 100 worst invasive species by the invasive species specialist group of the IUCN (Lowe et al. 2000). However, to date the eradication from nature of nutria has not been contemplated in this region and red-eared sliders are still widely kept in captivity.

Concluding remarks

ENI birds in this region do not follow the general idea of "climatic matching" since all are tropical. Also, some ENI birds in this region occupy different habitats from those used in their native range. Several of the species have already been noted as harmful to agriculture or natural environments; some are known as problematic elsewhere. More information is needed on the effects of these species in this region. Nevertheless, lack of information on harmful effects should not be an excuse for not acting swiftly against these species once they are discovered (Myers et al. 2000; Simberloff 2003). We also lack information on failed invasions and on propagule pressure, two lacunae that hinder our understanding of the observed invasion patterns (Cassey et al. 2004; Colautti et al. 2006).

Communication between Israel and its neighbors is lacking. It is possible that more non-indigenous species will be found in countries bordering Israel. Non-indigenous species are of global concern and dealing with them should also be promoted internationally (Mooney 1999).

Acknowledgments We thank Amos Bouskila, Ron Elazari-Volcani, Ohad Hatzofe, Shmuel Moran, Simon Nemtzov, Tzila Shariv, Yehudah L. Werner, and Yoram Yom-Tov for help in obtaining data. We thank the internal university fund (Tel-Aviv University) for supporting this research.

Appendices

Appendix 1: vegetation zones of the different ENI bird species in this region

Table A1 The average number of ENI bird species in each of the region's 34 vegetation zones. Vegetal zones after Zohary (1982)

Vegetation type and code	Area of vegetal zone (km$^{2)}$	Average num. of ENI birds
01: Climax of evergreen maquis and forests, destroyed and reoccupied by Mediterranean batha and garigue	3617.4	2.27
02: Stands of remnant evergreen maquis—under Mediterrranean conditions	650.0	1.71
03: Stands of remnant evergreen maquis—under Semisteppe conditions	302.2	1.89
04: Stands and remnants of *Pinion halepense*	55.0	0.83
05: Climax and scattered stands of *Quercion ithaburense*	227.0	1.69
06: As above, extremely devastated	156.0	1.82
07: As no. 6, but under semisteppe conditions.	46.7	1.26
08: Degraded maquis, often replaced by semisteppe bathas	141.7	1.61
09: Semisteppe chamaephytic and hemicriptophytic batha with only very sparse remnants of trees	245.7	1.64
10: Mediterranean batha and garigue on kurkar hills of the coastal plain	267.8	3.77
11: Mobile and stable sand dune and sand flat vegetation of the coastal plain and coastal Negev	1190.2	2.94
12: Sandy clay vegetation of the coastal plain	164.8	5.04
13: As above, but with remnants of *Quercus ithaburensis* trees or stands	352.6	4.14
14: Mediterranean semisteppe batha communities of the *Ballotetalia undulatae*	1221.7	2.46
15: Climax area of semisteppe batha (Ballotetalia) led by *Ziziphus lotus*	776.7	3.62
16: Climax area of semisteppe batha, led mainly by *Retama raetam*	308.3	3.45

Table A1 continued

Vegetation type and code	Area of vegetal zone (km$^{2)}$	Average num. of ENI birds
17: Alluvial or grumosolic plains. Climax vegetation mostly unknown	2457.2	3.65
18: Climax area of the Irano-Turanian dwarf shrub steppes dominated by *Artemisietea herbae-albae* comm.	2641.9	3.20
19: Climax area of typical Saharo-Arabian, almost no Sudano-Sindian species	1159.8	4.63
20: Area of Sudano-Sinidan enclaves (oases) consisting of the Zizipho-Balanitetum	53.2	2.20
21: Semisteppe veg. led mainly by *Salsoletum villosae*, recently partly converted (in the S.) to No. 22	62.3	2.50
22: Mediterranean and Saharo-Arabian salines.	283.5	2.85
23: Areas of Irano-Turanian vegetation on loess soil	1459.7	2.95
24: Sandy soil vegetation, mainly *Lolio multiflorae–Artemisietum monosperme* as climax community	591.0	2.48
25: Area of mosaic veg. of *Zygophylletalia dumosi* on the hills intersected by loessial valleys	624.8	2.38
26: Saharo-Arabian reg and hammada deserts with sparse patch veg. mainly in the ephemeral streambeds	2126.3	2.48
27: Saharo-Arabian veg. of the *Anabasetea* comprising large areas of sterile reg plains.	1982.1	1.09
28: Area of the *Acacietea raddianae* and *Hammadetea salicornicae* on fans along the Arava Valley	1955.6	3.78
29: Area of Lissan-Marl substrata, sterile or harboring *Salsoletum tetrandrae*	245.2	2.96

Table A1 continued

Vegetation type and code	Area of vegetal zone (km$^{2)}$	Average num. of ENI birds
30: Sand dune vegetation of the interior Negev comprising mainly *Anabaso articulatae arenarium*	103.4	1.27
31: Sands and sandy reg in the Arava Valley dominated by *Haloxyletum persici*	26.3	3.35
32: Area of south eastern coastal plain and westernmost foothills w. remnants of savanna-like veg.	426.0	2.62
33: Area of the *Populion euphraticae*	88.8	2.79
90: Built area	230.3	3.00
99: Unclassified	1217.0	5.16

Table A2 The different vegetal zones used for the six lumped vegetation and soil types

Lumped vegetation type	Vegetation codes used
Mediterranean forest and maquis	1–8
Mediterranean plains (batha)	9, 10, 15, 17, 32, 33
Sharo-Sindian desert	19–22, 25–29
Built area	90
Coastal and internal sands	11–13, 24, 30, 31
Steppe and Irano-Turanian vegetation	14, 16, 18, 23

References

Amitai P, Bouskila A (2001) Handbook of amphibians & reptiles of Israel. Keter Publishing House Ltd., Jerusalem (In Hebrew)

Beer R (1994) Black-headed conure – South American escapee nesting in Israel. Torgos 22:71–74 (In Hebrew)

Blackburn TM, Duncan RP (2001a) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. J Biogeogr 28:927–939

Blackburn TM, Duncan RP (2001b) Determinants of establishment success in introduced birds. Nature 414:195–197

Blackburn TM, Gaston KJ (1994) The distribution of body sizes of the worlds bird species. Oikos 70:127–130

Bodenheimer FS (1958) The present taxonomic status of the terrestrial mammals of Palestine. B Res Counc Israel 7B:165–187

Bouskila A (1986) On the danger of red-eared slider spreading in natural habitats in Israel. Hardun 3:27–30 (In Hebrew)

Bouskila A (2002) The class Reptilia. In: Dolev A, Perevolotsky A (eds) Endangered species in Israel, red list of threatened animals – vertebrates. Nature and parks Authority and The Society for the Protection of Nature in Israel, Jerusalem, pp 71–121 (In Hebrew)

Cadi A, Joly P (2003) Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). Can J Zool 81:1392–1398

Carter J, Leonard BP (2002) A review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor Coypus*). Wildlife Soc B 30:162–175

Cassey P (2001) Are there body size implications for the success of globally introduced land birds? Ecography 24:413–420

Cassey P (2003) A comparative analysis of the relative success of introduced land birds on islands. Evol Ecol Res 5:1011–1021

Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL (2004) Global patterns of introduction effort and establishment success in birds. Proc R Soc Lond B (Supplement) 271:S405–S408

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Dolev A, Perevolotsky A (2002) Endangered species in Israel, red list of threatened animals – vertebrates. Nature and parks Authority and The Society for the Protection of Nature in Israel, Jerusalem (In Hebrew)

Duncan RP, Young JR (1999) The fate of passeriform introductions on oceanic islands. Conserv Biol 13:934–936

Duncan RP, Blackburn TM, Sol D (2003) The ecology of bird introductions. Annu Rev Ecol Evol Syst 34:71–98

Dvir E (1985) Out of the cage. Teva Va-Aretz 27:10–16 (In Hebrew)

Dvir E (1988) Far from the cage – the rose ringed parakeet (*Psittacula krameri*) establishing in our area. Torgos 7:57–67 (In Hebrew)

Ebenhard T (1987) Introduced birds and mammals and their ecological effects. Swed Wildlife Res 13:5–107

Hatzofe O, Yom-Tov Y (2002) Global warming and recent changes in Israel's avifauna. Israel J Zool 48:351–357

Ilani G (1985) Zoological news: American turtles in Israel's waters. Teva Va-Aretz 27:37–38 (In Hebrew)

Jaffe S (1988) Climate of Israel. In: Yom-Tov Y, Tchernov E (eds) The zoogeography of Israel, the distribution and abundance at a zoogeographical crossroad. Dr. W. Junk Publishers, Dordrecht, the Netherlands, pp 79–94

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. P Natl Acad Sci USA 102:7198–7202

Klawinski PD, Vaughan RK, Saenz D, Godwin W (1994) Comparison of dietary overlap between allopatric and sympatric geckos. J Herpetol 28:225–230

Kolar CS, Lodge DM (2001a) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kolar CS, Lodge DM (2001b) Predicting invaders – response. Trends Ecol Evol 16:546

Leshem Y, Yom-Tov Y (1996) The magnitude and timing of migration by soaring raptors, pelicans and storks over Israel. Ibis 138:188–203

Lever C (1985) Naturalized mammals of the world. Longman Scientific & Technical, New York

Lever C (1987) Naturalized birds of the world. Longman Scientific & Technical, New York

Lever C (2003) Naturalized reptiles and amphibians of the world. Oxford University Press, Oxford

Lockwood JL (1999) Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. Conserv Biol 13:560–567

Lodge DM (1993) Species invasions and deletions: community effects and responses to climate and habitat change. In: Kareiva PM, Kingsolver JG, Huey RB (eds) Biotic interactions and global change. Sinauer Associates Inc., Sunderland, Massachusetts, pp 367–387

Long JL (1981) Introduced birds of the world. David & Charles, Newton, Australia

Long JL (2003) Introduced mammals of the world. CABI Publishing, Wallingford, UK

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) A selection from the Global Invasive Species Database. 100 of the World's Worst Invasive Alien Species. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens 12, December 2000. Updated and reprinted version: November 2004

Luiselli L, Capula M, Capizzi D, Filippi E, Jesus VT, Anibaldi C (1997) Problems for conservation of pond turtles (*Emys orbicularis*) in central Italy: is the introduced red-eared turtle (*Trachemys scripta*) a serious threat? Chelonian Conserv Biol 2:417–419

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Maurer BA (1998) The evolution of body size in birds. II. The role of reproductive power. Evol Ecol 12:935–944

Mendelssohn H, Yom-Tov Y (1999a) Fauna Palaestina: mammalia of Israel. Israel Academy of Sciences and Humanities, Jerusalem

Mendelssohn H, Yom-Tov Y (1999b) A report of birds and mammals which have increased their distribution and abundance in Israel due to human activity. Israel J Zool 45:35–47

Mooney HA (1999) The global invasive species program (GISP). Biol Invasions 1:97–98

Moran S (2003) Checklist of vertebrate damage to agriculture in Israel, updated for 1993–2001. Phytoparasitica 31: 109–117

Motro Y (2001) Risk assessment for the import of the exotic turtle, red eared slider (*Trachemys scripta*) to Israel. Internal report for the Research division in the Nature Reserve and Parks Authority, Jerusalem (In Hebrew)

Moulton MP, Sanderson JG (1997) Predicting the fates of Passeriform introductions on oceanic islands. Conserv Biol 11:552–558

Moulton MP, Sanderson JG (1999) Fate of Passeriform introductions: reply to Duncan and Young. Conserv Biol 13:937–938

Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. Trends Ecol Evol 15:316–320

Nemtzov S, Hatzofe O (2003) Priorities for dealing with terrestrial invasive vertebrates. Internal paper for the Israel Nature and Parks Authority, Jerusalem (In Hebrew)

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Paz U (1986) Plants and animals of the land of Israel – birds. Ministry of Defense, Tel-Aviv (In Hebrew)

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65

Qumsiyeh MB (1996) Mammals of the holy land. Texas Tech University Press, Lubbock, Texas

Rejmanek M, Reichard S (2001) Predicting invaders – comment. Trends Ecol Evol 16:545–546

Roll U, Dayan T, Simberloff D (2007a) Non-indigenous insect species in Israel and adjacent areas. Biol Invasions 9:629–943

Roll U, Dayan T, Simberloff, D, Goren M (2007b) Characteristics of the introduced fish fauna of Israel. Biol Invasions doi:10.1007/s10530-006-9083-8

Schmitz DC, Simberloff D (1997) Biological invasions: a growing threat. Issues Sci Technol 13:33–40

Shalmon B (1999) La-Teva Nolad report 1999 – on the status of wild animals in Israel. The Society for the Protection of Nature in Israel, Tel-Aviv (In Hebrew)

Shirihai H (1996) The birds of Israel. Academic Press, London

Shoham D, Mendelssohn H, Yom-Tov Y (1997) Range increase and breeding biology of the palm dove *Streptopelia senegalensis* in Israel. Israel J Zool 43:307–309

Simberloff D (1986) Introduced insects: a biogeographic and systematic perspective. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, pp 3–26

Simberloff D (1996) Impacts of introduced species in the United States. Consequences 2:12–23

Simberloff D (2003) How much information on population biology is needed to manage introduced species? Conserv Biol 17:83–92

Sol D (2001) Predicting invaders – comment. Trends Ecol Evol 16:544

Sol D, Lefebvre L (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90:599–605

Sol D, Timmermans S, Lefebvre L (2002) Behavioural flexibility and invasion success in birds. Anim Behav 63:495–502

Tchernov E (1988) The paleobiogeographical history of the southern Levant. In: Yom-Tov Y, Tchernov E (eds) The zoogeography of Israel, the distribution and abundance at a zoogeographical crossroad. Dr. W. Junk Publishers, Dordrecht, the Netherlands, pp 159–250

Vaughan RK, Dixon JR, Cooke JL (1996) Behavioral interference for perch sites in two species of introduced house geckos. J Herpetol 30:46–51

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542–557

Walker B, Steffen W (1997) An overview of the implications of global change for natural and managed terrestrial ecosystems. Conserv Ecol 1:2

Whittaker RJ (1998) Island biogeography. Oxford University Press, Oxford

Williamson M (1996) Biological invasions. Chapman and Hall, London

Yom-Tov Y (1988) The zoogeography of the birds and mammals of Israel. In: Yom-Tov Y, Tchernov E (eds) The zoogeography of Israel, the distribution and abundance at a zoogeographical crossroad. Dr. W. Junk Publishers, Dordrecht, the Netherlands, pp 389–409

Zohary M (1982) Plants of the Bible: a complete handbook to all the plants with 200 full-color plates taken in the natural habitat. Cambridge University Press, Cambridge