BIODIVERSITY RESEARCH

The effect of enemy-release and climate conditions on invasive birds: a regional test using the rose-ringed parakeet (*Psittacula krameri*) as a case study

Assaf Shwartz[1]*, Diederik Strubbe[2], Chris John Butler[3], Erik Matthysen[2] and Salit Kark[1]*

[1]*The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, The Silberman Institute Life Science, The Hebrew University of Jerusalem, Jerusalem 91904 Israel,* [2]*Evolutionary Ecology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610, Antwerp, Belgium,* [3]*Department of Biology, College of Mathematics and Science, University of Central Oklahoma, 100 N University Drive, Edmond, OK 73034-5209, USA*

ABSTRACT

Aim Some invasive species succeed particularly well and manage to establish populations across a wide variety of regions and climatic conditions. Understanding how biotic and environmental factors facilitate their invasion success remains a challenge. Here, we assess the role of two major hypotheses explaining invasion success: (1) enemy-release, which argues that invasive species are freed from their native predators and parasites in the new areas; and (2) climate-matching, which argues that the climatic similarity between the exotic and native range determines the success of invasive populations.

Location India, Israel and the UK.

Methods We studied the reproductive success of one of the most successful avian invaders, the rose-ringed parakeet (*Psittacula krameri*), in its native range (India) and in two introduced regions, varying in their climate conditions (Israel and the UK). We combined literature and field data to evaluate the role of predation pressure and climatic conditions in explaining the differences in reproductive success between the three regions.

Results We found significant differences in reproductive success between regions. In accordance with the enemy-release hypothesis, we discovered that while predation was the main factor responsible for the reduction of fecundity in India, it did not significantly affect the fecundities of parakeet populations in the two introduced regions. In accordance with the climate-matching hypothesis, we found that in the colder temperate UK, egg infertility was high, resulting in lower fecundities. Populations in both the warmer Mediterranean climate of Israel and in the native Indian range had significantly lower egg infertility and higher fecundities than the UK populations.

Main conclusions Our findings support both the enemy-release and the climate-matching hypotheses. While release from predators facilitates the reproductive success and therefore the invasiveness of parakeets in both the UK and in Israel, colder climate impedes reproduction and therefore the spread of parakeets in the UK.

Keywords
Biological invasions, birds, infertility, introduced species, predation, reproductive success.

Correspondence: Assaf Shwartz and Salit Kark, The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, The Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel. E-mail: shwar.a@mail.huji.ac.il, salit@cc.huji.ac.il Webpage: http://biodiversity-group.huji.ac.il/

INTRODUCTION

In the modern globalized world, a small number of species are successfully invading various regions throughout the world, causing both ecological and economic damages (McKinney & Lockwood, 1999). For a species to become invasive, it has to overcome several stages, including transport, introduction, establishment and spread. These are separate phases of the invasion process, and although much research has focused on the establishment stages, some recent studies have addressed the
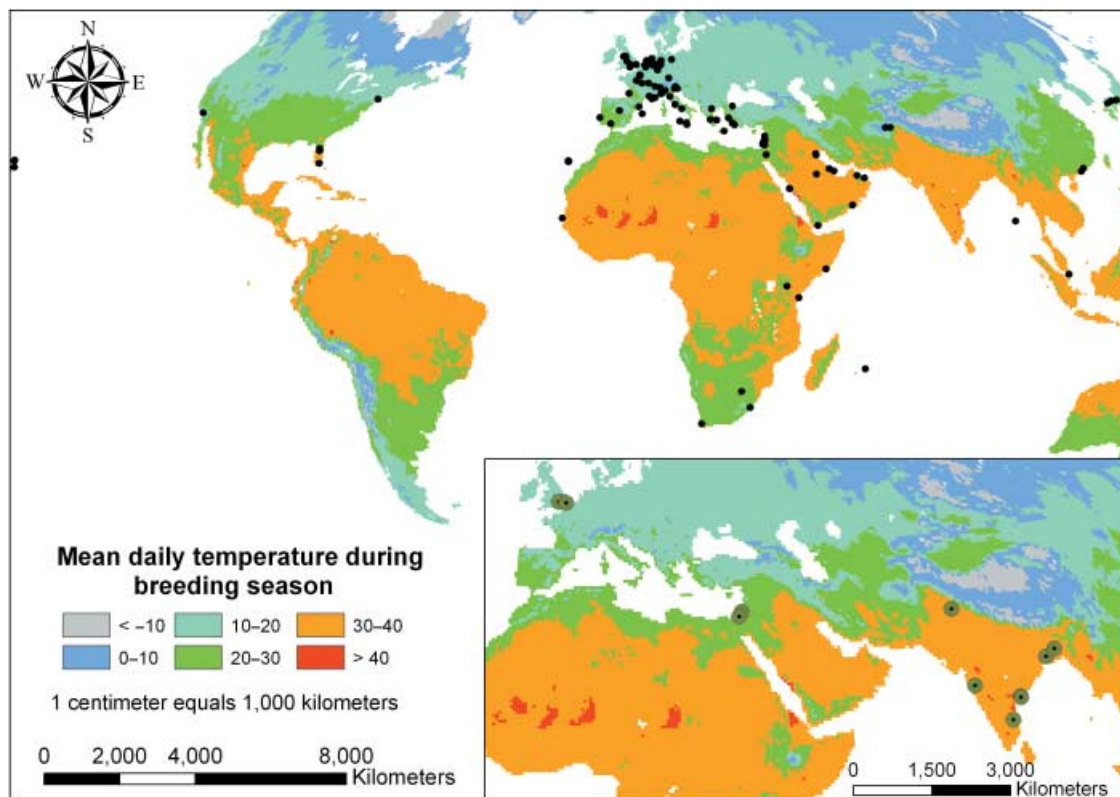
Figure 1 Known records of established rose-ringed parakeet populations (black dots) against a background of mean daily temperature (°C) during the breeding season (February to June). The inset map shows study sites (green marking) in the native range and introduced regions (based on WORLDCLIM; Hijmans *et al.*, 2005).

spread phase (Duncan *et al.*, 2003). The propensity of a species to spread and thus to become invasive depends on both species-specific traits (e.g. its dispersal capacity) and on the biotic and environmental conditions in the region invaded (Sakai *et al.*, 2001). In this paper, we focus on the role of environmental and biotic factors in shaping invasion success during the spread phase.

Several hypotheses have been raised to explain invasion success and two of the main hypotheses related to the influence of biotic and environmental conditions on invasion success are enemy-release and climate-matching. The enemy-release hypothesis argues that some introduced species succeed because they leave behind their co-evolved natural enemies when arriving in a non-native region (Colautti *et al.*, 2004; Liu & Stiling, 2006). The climate-matching hypothesis postulates that species will have higher invasion success when they are introduced to areas with climate more similar to that of their natural range (Williamson, 1996; Mack *et al.*, 2000). These hypotheses are often used to explain establishment success. Here, we examine whether the hypotheses are supported at the spread phase.

We study invasive populations of the rose-ringed parakeet (*Psittacula krameri*). Originating from Africa and Asia, the para-keet has become the most widely distributed parrot species in the world (Forshaw, 1989; Lever, 2005), having established populations in at least 35 countries on four continents (Butler, 2003; Lever, 2005). We use reproductive success to assess the invasion

success of the parakeets. Rose-ringed parakeets tend to have high juvenile and adult survival, in particular parakeets in the UK (Butler, 2003). Therefore, high reproductive success is one the key factors expected to facilitate spread (and thus invasiveness). We study the effect of climate-matching and enemy-release on reproductive success by comparing populations in two intro-duced regions (the UK and Israel) and in the native range (India). Surprisingly, few studies on vertebrates have made such comparisons, probably because of the difficulty in obtaining the detailed ecological information needed (MacLeod *et al.*, 2005). The invaded regions (the UK and Israel) provide an informative case study, since rose-ringed parakeets have mainly invaded temperate and Mediterranean areas around the world (Fig. 1). In both Israel and the UK, records of first establishment date from the mid-1960s and populations are currently large and rapidly growing (Shirihai, 1996; Butler, 2005). In this framework, we predicted that:

(a) Under the enemy-release hypothesis, average predation rates of rose-ringed parakeets in Israel and the UK will be lower than in native India.

(b) In temperate UK, due to climate mismatch, parakeets will have lower reproductive success than in Israel.

Birds can adapt their nesting preferences to reduce the effects of climate and predation (Albano, 1992; Eeva *et al.*, 2002). Since invasive birds tend to show behavioural plasticity (Sol *et al.*, 2002) this may confound results addressing climate-matching

Table 1 Location, year and number of nests examined in this paper in the native range (India) and in the two non-native regions (the UK and Israel).

Country	Research year	Cavity characteristics	Number of nests studied	Coordinates
*India	1966	–	24	18°31′N, 73°51′E
				12°54′N, 79°08′E
				16°34′N, 81°23′E
				22°32′N, 88°20′E
†India	1977–1978	–	66	16°23′N, 81°26′E
‡India	1990	–	10	23°42′N, 90°24′E
§India	1992	√	16	30°56′N, 75°52′E
¶UK	1999	–	12	51°27′N, 00°07′W
**UK	2001–2003	√	108	51°27′N, 00°07′W
††Israel	1983–1986	–	9	32°01′N, 34°47′E
‡‡Israel	2005–2006	√	47	32°05′N, 34°48′E

*Lamba, 1966; †Shivanarayan *et al.*, 1981; ‡Hossain *et al.*, 1993; §Dhanda & Dhindsa, 1998; ¶Pithon, 1998; **Butler, 2003; ††Dvir, 1988; ‡‡This paper.

and enemy-release. A lack of climate effect could be related to the fact that parakeets have adapted to the cold UK climate since their introduction by postponing their breeding season or by nesting in warmer cavities. In contrast, in warmer Mediterranean Israel, parakeets might benefit from breeding in cooler cavities to avoid hyperthermia during heat-spells. Accordingly, we also predict that:

(c) In the UK, parakeets will breed later than in warmer Israel, where they will breed early in the season to avoid hypothermia.

(d) In the UK, parakeets will prefer nesting in warmer cavities (south-facing openings), while in warm Israel, parakeets will show a preference for cooler, north-facing cavities. Parakeets nesting in these favourable cavities should have higher reproductive success.

METHODS

Study populations

We combined literature and field data to quantify and compare reproductive success of the rose-ringed parakeet in 19 populations in the native range (India) and in two introduced regions, south-eastern UK and central Israel (Table 1). All studies were performed in human-dominated environments, which are favoured by both native and exotic rose-ringed parakeets (Forshaw, 1989). Lamba (1966) collected data on breeding success of parakeets in a range of cities (Poona, Vellore, Akividu, Calcutta and Balaghat) across India. Dhanda & Dhindsa (1998) and Hossain *et al.* (1993) studied parakeets in the campuses of Punjab Agricultural University, Ludhiana University and Dhaka University in India. Shivanarayan *et al.* (1981) conducted field surveys in Maruteru, an agricultural region in India. In Israel, we collected data in the Yarkon Park Tel Aviv, Israel's largest urban park, which consist of several sub-environments (Shwartz *et al.*, 2008). Dvir (1988) monitored one population in an agricultural farm in the 1980s in an area south of Tel-Aviv. In the UK, Butler (2003) and Pithon (1998) undertook nest searches in the parks of Greater London, around the coast of Kent and in the town of Studland Dorset (2001–2003).

Although the three study regions (India, Israel and the UK) do not represent the full range of climates in which the parakeets were introduced, they are located along a northwest-southeast gradient of climate systems (based on the Köppen's classification) from tropical and subtropical climate in India through the Mediterranean climate of Israel to the temperate climate of the UK (Fig. 1).

Reproductive success

The monitoring of reproductive success was done in a similar way in all studies. All nests were examined in the field at intervals of 4 to 7 days by climbing up to the tree cavities and recording clutch size as well as the number of nestlings or fledglings in each nest. In case of egg or nestling loss, notes were made specifying the cause when known (e.g. infertility, predation, starvation). Data on cavity characteristics were collected in the more detailed field studies we conducted in Israel and the UK and one in the native range (Table 1), allowing us to investigate whether cavity characteristics reduce the effect of climate and predation.

We compared reproductive success (average number of fledglings per nest) between the native and the two introduced regions. We used general linear mixed models (GLMM) to test for pseudo-replications between studies. As no significant random effect (of study) was found, we used an equivalent and simpler linear model (Pinheiro & Bates, 2000). In all cases, both models produced the same qualitative results. A separate model was built for each of the three stages of reproductive success (clutch size, nestlings and fledglings) using the statistical package Genstat (Lawes Agricultural Trust, release 10.1, 2007).

In a second set of analyses we examined breeding failure. The probability of breeding failure was analysed separately for both the incubation and the fledgling stages. Egg failure was defined as any egg laid that failed to produce a nestling. Similarly, nestling failure was defined as a nestling that failed to fledge. To investigate whether probability of failure differed among the native and the two introduced regions, we built two separate GLMMs with a binomial error structure. Nest was included as a random term

Table 2 Two general linear models of factors affecting fledgling success of the rose-ringed parakeet in Israel ($R^2 = 0.58$, $n = 34$, $P < 0.001$) and in the UK ($R^2 = 0.15$, $n = 58$, $P < 0.001$). The effect size of factors is relative to the first level as presented in the table.

Fixed effect	Israel				UK		
	d.f.	Effect size ± SE	F	P-value	Effect size ± SE	F	P-value
Constant	1	2.26 ± 0.27	21.64	< 0.001	1.86 ± 0.17	11.08	< 0.001
Cavity orientation (North)	3	0	4.27	0.013	0	0.60	0.62
Cavity orientation (East)		−0.36 ± 0.47			−0.36 ± 0.42		
Cavity orientation (South)		−1.99 ± 0.60			−0.62 ± 0.54		
Cavity orientation (West)		−1.10 ± 0.54			−0.53 ± 0.47		
Clutch size	1	0.90 ± 0.16	34.00	< 0.001	0.45 ± 0.13	11.36	0.001
Cavity height	1	−0.11 ± 0.08	1.61	0.215	−0.06 ± 0.06	1.02	0.317
Tree diameter	1	−0.01 ± 0.01	0.26	0.616	−0.01 ± 0.01	0.32	0.573
Type of cavity (natural)	1	0	0.04	0.850	0	0.20	0.654
Type of cavity (woodpecker)		0.09 ± 0.45			−0.15 ± 0.33		

SE, standard error.

to account for repeated sampling within a nest, and region was included as a fixed effect (three-level factor: India, the UK and Israel). As our hypothesis (b) was that in the temperate UK parakeets will suffer from climate mismatch due to the cold climate compared with their native range, we also tested whether the average number of fledglings was correlated with the number of frost days using data obtained from the Met Office (2008). The average number of fledglings in each field study season (2001–2003) was calculated for each locality in the UK separately (Kent, S.E. London, S.W. London and Studland).

Finally, to compare the potential causes of egg and nestling failure between regions, we calculated the average infertility (mean number of infertile eggs per nest) as well as the average predation rate (mean number of preyed eggs and nestlings per nest). Since assumptions of normality were not met for infertility and predation, we compared mean fertility and predation between the three regions using the non-parametric Kruskal–Wallis test (Zar, 1999). We used a life-table approach to quantitatively asses the relative role of climate-matching and enemy-release. Life-tables begin at birth of individuals and provide age-specific survival and reproduction throughout individuals' lives. As this study focused on the effect of climate-matching and predator-release on parakeet reproductive success, we calculated separately the probability of an egg or nestling to reach the following stage in the breeding cycle and its probability to fail due to infertility and predation. In order to quantify the effect of climate we substituted the measured infertility rates of Israel and the UK by the rates associated with the Indian climate. In the same manner, to asses the importance of enemy-release, we replaced the stage-specific predation rates of Israel and in the UK with the predation rates in native India.

Phenology and cavity characteristics

We compared the timing of the breeding season between populations. For the non-native UK (breeding seasons 2001–2003) and for Israel (2005–2006), we calculated for each nest the number of days elapsed since the date the first egg was laid in each population during each breeding season. For each population we then calculated the mean variance in the date of first egg-laying and used it as an indicator of breeding season duration. Due to missing data for several nests, egg-laying dates were back-calculated from fledgling dates using the same incubation and fledging period (60 days) for the UK and for Israel (Cram& Simmons, 1997). We compared the mean variance in laying dates using a *t*-test after checking for normality and homogeneity of variances (Zar, 1999).

In addition, we investigated whether thermoregulation-related cavity parameters (see Table 2) affect reproductive success. Nesting in wide trees and cavities with small, sun-facing entrances (south) could improve thermoregulation during cold days (Wiebe, 2001; Paclik & Weidinger, 2007). Higher cavities and narrow entrances have been shown to reduce nest predation (e.g. Li & Martin, 1991; Albano, 1992). Cavity height was measured using a clinometer, and tree diameter at breast height (d.b.h.) was measured with a measuring tape. We measured the compass orientation of cavity entrances in the UK and in Israel. Data on cavity entrance diameter were unavailable for the UK. Instead, we used cavity type (natural versus woodpecker made), since in Israel natural cavities were found to have wider entrances (Mann–Whitney $Z = -4.80$, $n = 39$, $P < 0.001$).

We used two separate GLMMs to investigate whether cavity parameters affected reproductive success in the two introduced regions, while accounting for clutch size. Nest was used as a random term, but since we found no significant repeatability between nests we used general linear models (Pinheiro & Bates, 2000). All four explanatory cavity variables and their two-way interactions were entered into the model, since no significant collinearity was found between them. We then used a stepwise backwards procedure followed by forward procedure (Pinheiro & Bates, 2000) until only significant terms ($P \leq 0.05$) remained. In tables, statistics and *P*-value of significant terms were taken from the minimal model, whereas statistics and *P*-value of non-significant terms were obtained by fitting each non-significant

Table 3 Reproductive success parameters (mean ± standard error) of rose-ringed parakeets in the native range (India) and in the two non-native study regions (the UK and Israel).

	India	UK	Israel	F	d.f.	P-value
Number of eggs laid	3.83 ± 0.07* ($n = 116$)	3.75 ± 0.13* ($n = 89$)	4.05 ± 0.18* ($n = 39$)	1.13	2	0.324
Number of Nestlings	3.11 ± 0.20* ($n = 51$)	1.87 ± 0.15† ($n = 84$)	3.35 ± 0.23* ($n = 43$)	20.25	2	< 0.001
Number of fledglings	2.59 ± 0.24* ($n = 50$)	1.80 ± 0.12† ($n = 118$)	2.25 ± 0.20*† ($n = 52$)	5.70	2	0.004

*†A difference between letters within each row (a vs b) indicates pairs of means that significantly differ at the 0.05 level based on the Bonferroni test for multiple pairwise comparison of means.

term separately into the minimal model. All main effects entered in the model are presented in the tables with their mean effect size ± standard error (SE) and their significance.

RESULTS

Reproductive success

In total, 292 nesting attempts were monitored in the three regions combined (Table 1). Reductions in reproductive success occurred at different breeding stages in each of the study region. The average clutch size did not differ significantly between regions (Table 3). The number of nestlings was similar in India and Israel and was significantly lower in the UK (Table 3). In Israel, the number of fledglings was not higher than in the native range, while in the UK the number of fledglings was significantly lower than in India (Table 3). Egg failure was significantly different among regions (GLMM: Wald-statistic = 25.73, d.f. = 2, $P < 0.001$). The highest probability of egg failure on average was found in the UK (0.49), and was significantly lower in Israel and India (0.24 and 0.14, respectively). The number of infertile eggs was significantly higher in the UK compared with Israel and India (Fig. 2; Kruskal–Wallis $\chi^2 = 41.84$, d.f. = 2, $P < 0.001$). The probability of nestling failure was significantly different between the three regions (GLMM: Wald-statistic = 13.2, d.f. = 2, $P = 0.001$). While the probability of nestling failure was low in both the UK and in native India (0.07 and 0.13, respectively), it was significantly higher in Israel (0.33). In line with prediction (a), total predation differed significantly between the native range and the introduced regions (Kruskal–Wallis $\chi^2 = 13.53$, d.f. = 2, $P = 0.001$) and was highest in the native range (Fig. 2). In India, the probability of egg or nestling predation was 0.23, while in the UK and in Israel it was significantly lower (0.08 and 0.02, respectively). In the UK, as expected, there was a negative correlation between the number of frost days and the reproductive success ($r = -0.68$, $P = 0.03$, $n = 10$), supporting prediction b.

The life-table suggests that when the predation pressure in the UK and in Israel will be as high as in India (i.e. after 'switching off' the enemy-release advantage), this will result in a 21% reduction in the overall success rate in Israel and 17% reduction in the UK (Table 4). As expected, the infertility rates
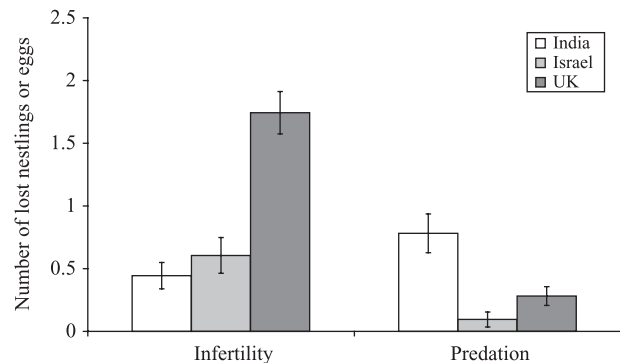

Figure 2 Mean number (± standard error) of infertile eggs, predated eggs and predated nestlings in the native range (India) and in the two introduced study regions (the UK and Israel).

associated with the warm Indian climate increase the overall success rate in cold UK considerably (64%). While in warmer Israel only a small difference (3%) in reproductive output is found when substituting the measured infertility rates by the rates associated with the warmer Indian climate (Table 4).

Phenology and cavity characteristics

Based on the mean variance in laying dates, the egg-laying period in Israel was shorter than in the UK ($t = -2.48$, d.f. = 138, $P = 0.014$). In line with prediction c, the breeding season in the UK began later than in Israel. In Israel, first egg-laying in all nests was recorded on 15 February, while in the UK it occurred 2 weeks later.

In contrast to prediction d, we found little evidence for an effect of cavity characteristics on reproductive success in the two introduced regions (Table 2). In the UK, cavities with warmer microclimate did not show higher reproductive success. Clutch size was the only significant variable explaining 15% of the variance in reproductive success (Table 2). However, in Israel, clutch size and cavity orientation explained 52% of the variance in fledgling success. After controlling for the positive effect of clutch size, nests with north-facing cavity entrances had higher fledgling success (3.0 ± 0.33 fledglings per nest), while south facing cavities had significantly lower success (< 1 fledgling per nest; Table 2).

Table 4 A life-table assessing the relative role of climate-matching and enemy-release as potential factors contributing to the invasion success of rose-ringed parakeets.

Stage	Proportion of original cohort surviving to the next stage			Enemy-release effect‡		Climate-matching effect‡	
	UK	Israel	India	UK	Israel	UK	Israel
Eggs*	1	1	1	1	1	1	1
Eggs after predation	0.94	0.97	0.80	0.80	0.80	0.94	0.97
Nestlings (i.e. hatched eggs)	0.54	0.85	0.88	0.54	0.85	0.88	0.88
Fledglings (i.e. all non-predated nestlings)	0.99	1.00	0.96	0.96	0.96	0.99	1.00
Overall success rate†	0.50	0.83	0.67	0.41	0.65	0.81	0.85
New: old success ratio				0.83	0.79	1.64	1.03
Change in overall success ratio§				−0.17	−0.21	+0.64	+0.03

*The proportion of eggs laid equals one in all regions being the first life stage in the table.

†Proportions calculated for predation and infertility only and not for other causes of reduction in reproductive success.

‡Assessing the relative role of infertility and predation was done by substituting the survival rates of the native range with the real ones at each of the invasive regions (the UK and Israel).

§Negative change stand for the reduction success ratio (due to predation) while positive for the improvement in success ration (due to better climate condition).

DISCUSSION

Enemy-release

In this paper, we compared populations of rose-ringed parakeets in the native range and in two introduced regions. As predicted by the enemy-release hypothesis (prediction a) we found that predation levels are significantly higher in India compared to the introduced regions (Fig. 2). The major nest predators in India were crows (Corvidae), owls (Strigiformes) and snakes (Lamba, 1966; Shivanarayan *et al.*, 1981; Hossain *et al.*, 1993; Dhanda & Dhindsa, 1998), while in the UK the only recorded predator was the grey squirrel (*Sciurus carolinensis*) and in Israel it was unknown. These results are supported by information from the literature on potential parakeet predators. In India, sixteen owl species are small enough to enter parakeet nests (Rasmussen & Anderton, 2005). In the study areas in Israel and the UK there is only one owl species (scops owl, *Otus scops* and little owl, *Athene noctua*, respectively) that could potentially enter parakeet nests, and these owls are mostly insectivorous and rarely predate on cavity-nesting birds (Cramp & Simmons, 1985). In the introduced regions, only one crow species has body size similar to parakeets, but it tends to be larger, and can therefore probably not enter most of the parakeet cavities (Cramp & Simmons, 1985). The number of snake species is larger in India compared to the UK or Israel (Coborn, 1991). As expected under the enemy-release hypothesis, the density of potential predators is higher in the native range.

The effect of climate on reproductive success

As expected under the climate-matching hypothesis, the UK parakeets have reduced breeding success compared with their native range, mostly due to increased egg infertility. In line with prediction b, we found reduced reproductive success in colder UK but not in warmer Israel. In the UK infertility was the most dominant cause of failure in reproductive success and more than 40% of the eggs laid were infertile, compared with only 10% in India and 12% in Israel. Rates of infertility in the UK are exceptionally high, since infertility of avian eggs averages about 10% (Koenig, 1982). Temperature has a unimodal effect on avian embryonic development, and both high and low temperatures increase infertility (Webb, 1987). Eggs exposed to low temperatures both in the laboratory (Hep *et al.*, 2006) and in the wild (Eeva *et al.*, 2002) exhibit increased infertility when temperature drops. Therefore, we suggest that high egg infertility in the UK can be due to the cold climate (Fig. 1).

The climate-matching hypothesis was also supported by the negative correlation we found in the UK between the number of frost days and reproductive success. In warmer Israel, where few to no frost days a year occur in the study area, parakeets experience lower average infertility, suggesting that they do not suffer from climate mismatch. Moreover, Strubbe & Matthysen (unpublished data) found that rose-ringed parakeet establishment success is lower in colder regions across Europe, and that climate-matching also plays a role at earlier invasion stages. Although parakeets can succeed in establishing self-sustaining populations in relatively cold regions (e.g. in central Europe), we find that parakeet breeding performance is not as good as in warmer regions. In colder regions, the spread of established parakeet populations could be impaired by low reproductive success. Global warming may reduce the climate mismatch and facilitate invasive spread of rose-ringed parakeets.

Rose-ringed parakeet reproductive success is clearly influenced by both climate factors and by enemy-release. Under the climate-matching hypothesis, we predicted that climate will have a strong impact on the UK parakeets, but not on Israel's parakeets. This is supported when using a life-table approach. In the UK, climate-matching contributes 64% to the parakeet reproductive success, while in warmer Israel the difference is only 3%. In

Phenology and cavity characteristics

Given that over four decades have passed since their initial introduction in Israel and in the UK, parakeets could demonstrate behavioural plasticity and may have adapted to their new habitat. Indeed, as predicted (prediction c), we found that in colder UK, parakeets start breeding later than in Israel. However, compared with the native range, where egg-laying occurs when mean temperatures range between 21–27 °C (Hijmans *et al.*, 2005), the UK parakeets start breeding in very cold conditions (average temperature of 4.3 °C, Hijmans *et al.*, 2005). As the high egg infertility of the UK population is likely caused by the cold climate, parakeets there may benefit in the future from shifting their breeding to later in the season. Other cavity nesters are known to adjust their breeding season to avoid cold conditions (Cucco *et al.*, 1992) or food shortage (Perrins & McCleery, 1989). In the UK, Pithon (1998) found that the parakeet diet consists of ornamental trees and especially of seeds found in artificial bird feeders during the winter. This flexibility in food preference and the usage of artificial bird feeders might be paradoxically maladaptive, as it enables the parakeets to survive and to begin breeding at the end of the cold European winter. Thus, behavioural flexibility in feeding may actually lead to a reduction of parakeet breeding success in the UK. It is interesting to note that a comparison of the duration of the egg-laying period between the UK and Israel shows that the breeding season in the UK is longer. This difference is due to the heavier tail in the distribution of laying dates in the UK (skewness in the UK populations combined is 0.80 compared with 0.14 for Israeli parakeets). This suggests that some of the UK parakeets breed later than the bulk of the population and are possibly undergoing an adaptation process.

In contrast with prediction d, we found no evidence that parakeets in the UK had higher reproductive success when breeding in cavities that are better insulated (Table 2). We suggest that the cold English climate is extreme for parakeet embryos, which leads to egg failure even in the relatively warmer cavities. In contrast, parakeets in Israel that breed in north-facing cavities have a significantly higher reproductive success, likely related to the warm climate, as parakeets may suffer from hyperthermia and show corresponding behaviour. Hyperthermia has been suggested several times to have an effect on cavity-nesting species, including parrots (e.g. Seixas & Mourao, 2002).

Breeding in Israel is characterized by high unexplained nestling loss (35%), which caused the majority of reproduction failure. Several factors could explain the high nestling loss in Israel, including predation, parasites and diseases, food shortage, sibling rivalry or competition with other cavity-nesters. Predation is usually characterized by the loss of all nestlings (Hossain *et al.*, 1993) and by distinctive behaviours of parents, and this was only observed once in our study. We found evidence for diseases or parasites in only two nests. There was no evidence that either sibling rivalry affected reproductive success, since larger broods had lower mortalities than smaller ones (ANOVA $F = 3.33$, d.f. = 2, $P = 0.05$) in contrast to the sibling rivalry predictions (Mock & Parker, 1997). We could not directly test the 'food shortage' hypothesis in this study, but a radio tracking study of six pairs during breeding indicates that food sources are abundant in the study site (A. Shwartz, unpublished data). In accordance with the competition hypothesis, reduction in fledgling success was significantly higher (Mann–Whitney $U = 48$, $P = 0.05$) in cavities which were occupied by other species directly after the parakeets had finished their breeding. The Yarkon Park is a cavity-poor environment and hosts a large population of exotic cavity-nesting species (Shwartz *et al.*, 2008). Competition for cavities was observed mostly with the invasive common myna (*Acridotheres tristis*) and the native house sparrow (*Passer domesticus*). Constant nest guarding by the parakeet was necessary to protect their broods. Nestling death may thus have resulted from the reduction of provisioning rates due to nest guarding (Orchan, 2007), but further investigation is required.

Many studies in biological invasion aim to improve our understanding of invasion mechanisms (Richardson & Pyšek, 2008). The availability of new data sets, such as the new DAISIE database (DAISIE, 2008), and better computing power lead to new advances in understanding invasiveness (Richardson & Pyšek, 2008). Thuiller *et al.* (2005) showed that integrating approaches using climatic suitability models and accounting for propagule pressure improved the explanatory power in predicting invasion success. In this study, we showed that climatic conditions and predation had opposite effects. Although parakeets in the UK suffered from lower fecundities probably due to cold climate condition, their population were still growing (Butler, 2003) due to enemy-release. Thus, comparisons between native and introduced populations while accounting for various factors such as climate, predation, propagule pressure and behavioural flexibility will help us obtain more correct understanding of invasion patterns.

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Editor: David Richardson