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Reproductive timing as a constraint on invasion success in the Ring-necked parakeet (*Psittacula krameri*)

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Abstract Climate similarity favors biological inva-
sion, but a match between seasonality in the novel
range and the timing of life cycle events of the invader
also influences the outcome of species introduction.
Yet, phenology effects on invasion success have
generally been neglected. Here we study whether a
phenological mismatch limits the non-native range of
a globally successful invader, the Ring-necked para-
keet, in Europe. Given the latitudes at which parakeets
have established across Europe, they breed earlier than
expected based on breeding dates from the native
Asian range. Moreover, comparing the breeding dates
of European populations to those of parakeets in the
native Asian range, to five native breeding bird species
in Europe and to the start of the growing season of four
native European trees shows that the discrepancy
between expected and actual breeding phenology is
greater in northern Europe. In northern European
populations, this temporal mismatch appears to have
negative effects on hatching success, and on

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population growth rates in years that are colder than average in the first six months. Phenological mismatch also can explain why parakeets from African populations (that are more likely to breed in autumn) have been poor invaders compared to parakeets from Asia. These lines of evidence support the hypothesis that the reproductive phenology of the Ring-necked parakeet can be a limiting factor for establishment and range expansion in colder climates. Our results provide growing support for the hypothesis that the match between climate seasonality and timing of reproduction (or other important life cycle events) can affect the establishment success, invasive potential and distribution range of introduced non-native species, beyond the mere effect of climate similarity.

Keywords Phenology · Climate · Invasive species · Adaptation · Urban environment · Pet trade · Parrots

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Introduction

Invasive species are generally accepted as one of the main threats to global biodiversity, ecosystem services, agriculture and public health (Mack et al. 2000; Sala et al. 2000; Vitousek et al. 1996; Paini et al. 2016). Identifying the invasion dynamics and underlying mechanisms allowing introduced species to establish viable populations in new places is crucial to prevent and mitigate future and ongoing biological invasions (Kolar and Lodge 2001). Several hypotheses have been raised to explain how biotic and abiotic conditions influence invasion success. Among those, climate matching is one of the most-supported hypotheses (Jeschke 2014). The climate-matching hypothesis states that species will have higher invasion success when they are introduced to areas with a climate more similar to that of their natural range. However, most climates are seasonal, so for successful invasion the changes in biotic and abiotic conditions over time in the novel range need to be synchronized with the timing of life cycle events of the invading species, such as the timing of reproduction.

Timing of reproduction is considered to be one of the major life history traits influencing the adaptation of native species to local characteristics of their environment (Lambrechts and Visser 1999). Mistiming between reproduction and maximum resource availability can lead to significant fitness reduction, e.g. due to food shortage for developing offspring (Thomas et al. 2001). Given the importance of timing for the adaptation of native organisms to local environments, the same should be true for invasive species. Depending on the environmental cues used and the flexibility in responses to that information, the phenology of invasive species may either match the novel seasonal changes correctly, or mismatch to a lesser or greater extent.

Nonetheless, the phenology of invasive species has generally been neglected in invasion biology as a factor which may influence the invasion success, with a few exceptions. There is growing evidence that phenology can play an important role in invasion success of plants and vertebrates (Gurvich et al. 2005; Wolkovich and Cleland 2010; Godoy and Levine 2014; Sanz-Aguilar et al. 2015). For instance, in their study on (sub)tropical invasive passerines in southern Spain, Sanz-Aguilar et al. (2015) found that these have breeding seasons that continued into, or were even restricted to, late summer and autumn (August to October), thereby breeding much later than ecologically comparable native species. It is likely that this unusual yet successful timing of reproduction was facilitated by changes in land use (rice production in late summer), which created the opportunity to breed so late. This suggests that there was an empty *temporal* niche (i.e. the temporal position a species has in its environment), which was filled by the invasive species instead of by native species. Since the literature showed that these invasive species already bred in these same months in their native ranges, this late breeding appeared not to be a plastic response to this opportunity (Sanz-Aguilar et al. 2015). Hence, this study provides evidence that reproductive timing can positively affect invasion success. At the same time,

the rather fixed nature of the reproductive phenology (the invaders maintained their phenology of their original ranges) suggests that it could also act as a selective filter: if the invasive species would not breed in autumn in its native range (e.g. only in spring like competing natives, or even only in winter), they might not have established (Sanz-Aguilar et al. 2015).

In this study we investigate the possible role for reproductive phenology in the invasion success of the Ring-necked parakeet (*Psittacula krameri*). This species of tropical and subtropical latitudes has established independent populations in many countries around the world (Lowe et al. 2000; Menchetti and Mori 2014; Pârâu et al. 2016) as a result of releases and escapes of individuals sold as pets. The species is regarded as one of the 100 most invasive species in Europe (DAISIE 2008), showing a remarkable population growth rate of about 19% per year on average (i.e. a doubling of the population every four years) in many western and southern European countries (Pârâu et al. 2016). On the other hand, the species is markedly absent from many northern and eastern European countries. While the number of parakeets imported into those countries is also lower (i.e. lower propagule pressure, see Jackson et al. 2015), this absence can also partly be explained by climatic differences. Strubbe and Matthysen (2009a) found a relationship between establishment success and the number of frost days, such that in Europe most introductions in areas with over 50 frost days per year have failed. Intuitively, this relationship could be explained by increased adult mortality during colder winters. Although adult parakeets have been reported to suffer from cold winter temperatures at the individual level (Schürmann 1981; Temara and Arnhem 1996; Pollheimer et al. 2006; 69% of parakeets show signs of frost bite on feet—M. Braun pers. obs.), reports of large-scale declines due to cold spells at the population level are rare. Indeed, Thabethe et al. (2013) found that adult ring-necked parakeets show no hypothermia at 5 °C, and the species may thus be better able to withstand cold temperatures than would be expected from its largely (sub)tropical origin.

Alternatively, as the species starts reproduction quite early in spring, Shwartz et al. (2009) suggested that low temperatures might act on parakeet breeding success rather than on adult survival. In support of this, they found that in the relatively cool United Kingdom about half of the eggs laid did not hatch, whereas hatching success is high in warmer countries such as Israel (non-native) and India (native). Cold weather in early spring could also negatively influence the development of food resources the parakeets use (fruits, flowers, buds), and the energy budgets of chicks (lower uptakes of energy due to lower food availability and shorter days, greater expenses to thermoregulation due to lower ambient temperatures). Such negative effects of low temperatures on breeding success would be intensified if individuals do not fully adjust to the seasonality of temperate latitudes compared to their native range, and therefore breed too early at higher latitudes.

To explore the often neglected possibility that phenological timing can be an additional driver of invasion success, here we test the hypothesis that the lower establishment success of the parakeets in colder climates as found by Strubbe and Matthysen (2009a) could be due to their mismatched reproductive timing. To this end, we collected published and new data on the reproductive timing of Ring-necked parakeet populations along a latitudinal gradient across Europe. This allowed us to establish a relationship between reproductive timing and latitude for parakeets in the invaded European range. We then compared this relationship to similar relationships for (1) parakeets in their native range, (2) native bird species in Europe, and (3) the beginning of the growing season of native trees in Europe. If parakeets breed earlier than expected in northern parts of their novel distribution range, we predict that this relationship will have a lower slope for the parakeet than for native birds and native trees.

Materials and methods

Study species and study area

The Ring-necked parakeet (*Psittacula krameri*) is a widely distributed species of the family Psittacidae, with four subspecies—two African (sub-Saharan) and two Asian (Indian sub-continent) (Juniper and Parr 1998). Based on genetic comparisons, parakeets in Europe predominantly originate from the Asian subspecies (Jackson et al. 2015). In Asia, parakeets are most common in anthropogenic landscapes such as agricultural and urban areas, reaching up to 1600 meters of altitude near the Himalayas, although mostly occurring below 900 m. The invasion of Europe is

characterized by a strong niche shift towards colder areas (Strubbe et al. 2015).

For nesting, Ring-necked parakeets normally use natural cavities in trees as well as cavities made by other birds, preferably in the higher part of the trees (Orchan et al. 2013). In the native Asian range, pair bond formation occurs between September and December, coinciding with a decrease in daylight hours (Sailaja et al. 1988). In January, they begin spending more time around their nest holes and show intensified courtship behavior, which culminates in successful copulation by mid-February. The majority of eggs are laid between late February and March, by mid-April most chicks have hatched, and the majority of chicks fledge between the end of May and early June (Krishnaprasadan et al. 1988).

For this study we combined published and unpublished phenological data from nine non-native Ring-necked parakeet populations (see Table 1), varying in latitude and climate (Fig. 1): Tenerife (Canary Islands (Spain): subtropical), Seville (Spain: Mediterranean), Florence (Italy: Mediterranean), populations in Central Israel (Mediterranean), London (United Kingdom: maritime temperate), Brussels (Belgium: maritime temperate), Haarlem (The Netherlands: maritime temperate) and Wiesbaden and Heidelberg (Germany: continental temperate). We also obtained phenological data from the native area (India).

Methodology

As Ring-necked parakeets typically breed in natural tree cavities, often at a considerable height, direct data on the timing of reproduction, such as egg laying date and fledgling date, are scarce. For some populations we therefore collected two additional, indirect types of phenological data: maximum number of birds counted at communal roosts directly after the breeding season (i.e. when most fledglings have joined the adults), and timing of post-breeding molt (see Table 1). Even though this introduces heterogeneity in the data, this does allow us to compare a large number of populations across a continent-wide latitudinal gradient.

Date of first egg laying (non-native range)

Occupied cavities and nest boxes were checked every three to four days to record when eggs were laid (Shwartz et al.

2009; Braun and Wink 2013). If there was more than one egg at the first encounter, then the laying date of the first egg was back-estimated, taking into account that the laying interval is 1–2 days (Braun and Wink 2013). The data from nests across the entire breeding season were averaged to get a population estimate of date of first egg laying.

Date of first fledging

Occupied cavities (Israel) were checked every three to four days with insertable cameras to count the number of fledglings (Shwartz et al. 2009). Fledging was assumed to have started when the number of fledglings decreased between checks without indications of mortality. If all chicks had fledged between two checks, the median date was used as an approximation of exact fledging date. A second, more indirect method used (Italy) was to record whether parents still visited the nest cavity to feed the chicks. Nests were observed for several hours every two weeks. The median date between the last date with parents and the first date without parents was used as estimate of fledging date. The data from nests across the entire breeding season were averaged to get a population estimate of date of first fledging.

Maximum roost counts

Ring-necked parakeets spend the night in communal roosts, with the exception of females tending nests, nestlings, and recently fledged chicks (Butler 2003; A. Shwartz pers. obs.). When fledglings are capable of sustained flight, they follow their parents to the roost. Consequently, changes in roost size during spring and early summer can reflect when eggs were laid. This could thus serve as a reliable proxy of the average timing of reproduction of the entire population. Moreover, the relative ease of counting roosting birds also enables replication across different populations and countries, such that geographical comparisons become feasible. At all sites, parakeets were counted from well-before the first individuals arrived at the roosting trees, until well after the last birds had arrived. When possible, incoming parakeets were counted individually, but if the flock size was too large numbers were estimated. We discarded movements between roosting trees and subtracted any individuals who left the roost (mostly to return later). We use the date of the maximum roost count as proxy for average reproductive timing.

Table 1 Overview of the data used to make Fig. 3

Species	Population	Date	Data type	Latitude	Year	Sample size	Source
R.-N. parakeet	Tenerife	168.4	Molt	28.29	2014	18	Dailos Hernández-Brito & Álvaro Luna
R.-N. parakeet	Israel	166	Count	31.05	2014	13	Yariv Malihi & Asaf Kaplan
R.-N. parakeet	Israel	62.5	Eggs	31.05	2005	9	Assaf Shwartz
R.-N. parakeet	Israel	133.7	Fledge	31.05	2005	9	Assaf Shwartz
R.-N. parakeet	Israel	67.7	Eggs	31.05	2006	12	Assaf Shwartz
R.-N. parakeet	Israel	137.9	Fledge	31.05	2006	23	Assaf Shwartz
R.-N. parakeet	Seville	173	Count	37.39	2011, 2014	33	Pim Edelaar & Álvaro Luna
R.-N. parakeet	Seville	169.2	Molt	37.39	2011, 2013	102	Dailos Hernández-Brito, Pim Edelaar & Álvaro Luna
R.-N. parakeet	Florence	150.8	Fledge	43.77	2010	8	Emiliano Mori & Mattia Menchetti
R.-N. parakeet	Heidelberg	78.1	Eggs	49.39	2006–2008	25	Michael Braun
R.-N. parakeet	Wiesbaden	79	Eggs	50.06	1995, 1996	113	Zingel (1997)
R.-N. parakeet	Wiesbaden	215	Count	50.06	2004–2008, 2014	170	Detlev Franz
R.-N. parakeet	Wiesbaden	184.8	Molt	50.06	2004–2005, 2007–2008	168	Detlev Franz
R.-N. parakeet	Haarlem	172	Count	52.38	2014	15	Sovon
R.-N. parakeet	Brussels	175	Count	50.85	2014	10	Diederik Strubbe
R.-N. parakeet	London	85.2	Eggs	51.52	2001–2003	108	Butler (2003)
R.-N. parakeet	London	84.6	Eggs	51.51	2010	37	Dave Parrott/DEFRA
Serinus serinus		91	Eggs	40.41			Cramp et al. (1994)
Serinus serinus		129	Eggs	52.52			Cramp et al. (1994)
Cyanistes caeruleus		104	Eggs	43.3			Cramp and Perrins (1993)
Cyanistes caeruleus		117.5	Eggs	56.26			Cramp and Perrins (1993)
Ficedula hypoleuca		129	Eggs	48			Both and te Marvelde (2007)
Ficedula hypoleuca		141	Eggs	55			Both and te Marvelde (2007)
Sturnus vulgaris		96	Eggs	40			Both and te Marvelde (2007)
Sturnus vulgaris		115	Eggs	55			Both and te Marvelde (2007)
Parus major		105	Eggs	40			Sanz (1998)
Parus major		122	Eggs	55			Sanz (1998)
four native trees	Florence	81.5	BGS	43.77			Rötzer and Chmielewski (2001)
four native trees	Heidelberg	96.4	BGS	49.39			Rötzer and Chmielewski (2001)
four native trees	Wiesbaden	98.3	BGS	50.06			Rötzer and Chmielewski (2001)
four native trees	Brussels	95.8	BGS	50.85			Rötzer and Chmielewski (2001)
four native trees	London	95.7	BGS	51.51			Rötzer and Chmielewski (2001)

Table 1 continued

Species	Population	Date	Data type	Latitude	Year	Sample size	Source
four native trees	Haarlem	99.1	BGS	52.38			Rötzer and Chmielewski (2001)

For each species and location of the parakeet population involved, we list the date (number of days since January 1st) for the occurrence of each type of phenological event, the approximate latitude, in which years the data was collected, and the origin of the data

Fig. 1 Location of the populations included in this study

Timing of post-breeding molt

The Ring-necked parakeet has a complete post-breeding molt (Butler and Gosler 2004). It is therefore expected that if the breeding period differs between populations, the timing of post-breeding molt will also differ. During the post-breeding season primary feathers were collected underneath the roost almost daily. Collected primaries were classified according to their position (1 = inner primary to 10 = outer primary). For this we measured them with a ruler and also evaluated their shape and color characteristics in order to assign each primary to a certain position. We used the size and general aspect of the primary feathers of six dead parakeets as a reference. Primary molt typically begins at primary 6 and then spreads out in both directions (Butler and Gosler 2004; Pyle 2013). Because we did not always manage to obtain complete coverage for the later part of molt, we calculated the average date of molt in the population of primaries 5, 6 and 7 (i.e. initiation of molt).

Date of egg-laying in the native Indian range

We studied 46 clutches in various natural history collections which were collected across virtually the entire latitudinal range of the Indian native distribution

(from 12°N to 34°N). We used the date of clutch collection as a proxy for laying date since most clutches are probably collected in the very early breeding stage or even before the clutch is completed (since for incubated eggs it is harder to blow out their contents: Scharlemann 2001).

Phenological data of native birds

We searched the literature for data on the date of first egg laying (first broods only) along latitudinal gradients for other, native bird species living in the same (western Eurasian) study area in order to compare their reproductive timing with that of the parakeet. Since there are no native parakeets in Europe and there are also no real ecological equivalents (hole-nesting generalist feeding mainly on buds, flowers, fruits and seeds), we used data from native passerines whose reproductive timing is adapted to the local climate and phenological development of the vegetation (sensu Pearman et al. 2010). Many estimates found in the literature were rather qualitative and imprecise and therefore unsuitable (e.g. "first week of April in southern Europe, one month later in northern Europe"). So we used only data for five species for which more detailed information was available (Table 1; only the extremes of the latitudinal range for which we

have data are given): the Blue tit (*Cyanistes caeruleus*, from Cramp and Perrins 1993), the Great tit (*Parus major*, Sanz, 1998), the Serin (*Serinus serinus,* from Cramp et al. 1994), the Pied flycatcher (*Ficedula hypoleuca*) and the Common starling (*Sturnus vulgaris*, both from Both and te Marvelde 2007). For Blue tit, we excluded data on timing from northern Africa, as this deviated strongly from the rest of Europe and because the taxon occurring in that zone is currently considered to be a different species (the African blue tit, *Cyanistes teneriffae*).

Phenological data of native trees

Data on tree phenology have been collected using a standardized protocol in tens of phenological gardens across Europe which ranges across 28 latitudes from Scandinavia to Macedonia and across 37 longitudes from Ireland to Finland in the north and from Portugal to Macedonia in the south. Data have been collected for a large set of tree species planted in these gardens over more than 50 years (Chmielewski et al. 2013). In these plots, phenology has been shown to have strong relationships with latitude, longitude and altitude (Chmielewski and Rötzer 2001; Rötzer and Chmielewski 2001). As in Chmielewski and Rötzer (2001), we calculated the beginning of the growing season for each of the study sites based on the leaf unfolding of a selection of four widespread species (*Betula pubescens, Prunus avium, Sorbus acuparia* and *Ribes alpinum*) as observed between 40–70°N and 10°W–30°E. The equation-based calculation takes into account geographical location and altitude. Because of the geographical coverage of the equation, the beginning of the growing season could however not be calculated for Tenerife, Israel and Seville.

Data analysis

We expect that all types of phenological data on invasive parakeets (date of first egg laying, date of fledging, date of maximum number at roost count, and date of molt) reflect the timing of reproduction along the latitudinal gradient. Thus, all those relationships would be characterized by similar slopes but different intercepts. We therefore estimated the overall slope of the regression line between timing of reproduction and latitude by ANCOVA, with date as the dependent variable and latitude as continuous explanatory variable, controlling for type of data as categorical explanatory variable. If parakeets breed relatively early in the northern part of their invasive European range, this slope should become shallower.

For parakeets in the native range we regressed egg collection date against latitude. We omitted the data from two outlier clutches because it was unclear whether the date was correct: one clutch from latitude 6°N collected on 27 November and one clutch from latitude 28°N collected on 10 September—all other clutches were collected in a concentrated time span between 28 December and 19 April. Omitting these two data points reduced the slope, and therefore resulted in a more conservative test.

For the native European birds, the quality and amount of data varied greatly among species, and a quantitative comparison of slopes would invoke a level of precision which is unwarranted. We therefore calculated the probability that the slope for the parakeet would be shallower than the slope for the native birds, based on the binomial distribution. The data on the native European birds come from different years, and most of them are older than those from the parakeets. However, annual variation in timing of breeding and any shifts in breeding time due to e.g. climate change should have more effect on the intercept of and the scatter around the relationship between date and latitude, and not so much on the slope itself, which is what we focus on here.

To explore the phenology of the native, European trees we regressed the calculated start of the growing season against latitude in order to obtain the slope. Again, we predict that the slope for invasive parakeets will be shallower than the slope for the native trees.

Results

Native Indian parakeets start egg-laying later towards the north (Fig. 2: $R^2 = 0.23$, $F_{1,41} = 12.0$, $p = 0.0013$) by on average 2.19 days per degree latitude (95% CI 0.914–3.470). This relationship between latitude and breeding date does not hold when extrapolating to European latitudes, as invasive parakeet populations start egg-laying earlier than native parakeets breeding at comparable latitudes (Fig. 2). Moreover, while breeding dates correlate with latitude in Europe as well, the slope is much smaller in the invasive range (Fig. 2).

This shallow slope for invasive parakeet populations compared to native populations is generalized and confirmed in our analyses of the four types of reproductive phenological data (egg laying, fledging, roost count and molt) as a function of latitude (Fig. 3). All these data types have very similar slopes (with maximum roost counts and initiation of molt generally coinciding in time). The overall slope of the relationship between breeding data and latitude for invasive parakeets is only 0.90 days/° (N = 17, R^2 = 0.97, $F_{1,12}$ = 8.90, p = 0.011). This is much lower than the mean (2.19 days/°) and outside the 95% confidence interval (0.914–3.470 days/°) for parakeets from the native range.

Notably, the slope of the relationship between breeding dates and latitudes across Europe is smaller for invasive parakeets (0.90 days/°) than for native European birds (1.55 days/°, Fig. 3). Even though the native species show variation in slopes, all five native species have steeper slopes than the invasive parakeets, on average 1.73 times as steep as that of the parakeet. The probability (p value) for this result is $(0.5)^5$ = 0.036. Over the range of the 24.1° latitude that span our study area, native breeding birds breed on average 37.3 days later in the north than in the south, compared to only 21.6 days later in Ring-necked parakeets. An even larger difference would result if we would use the slope (2.19) from the native Indian range (Fig. 2) to predict parakeet breeding dates across the invaded Europe range.
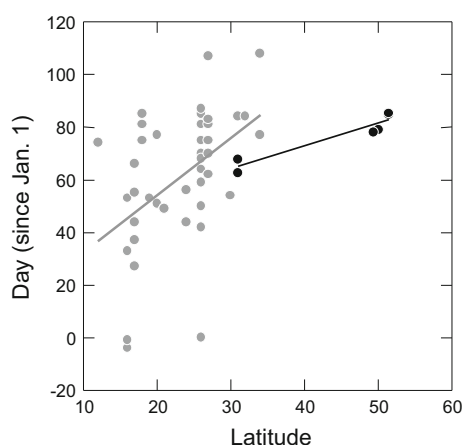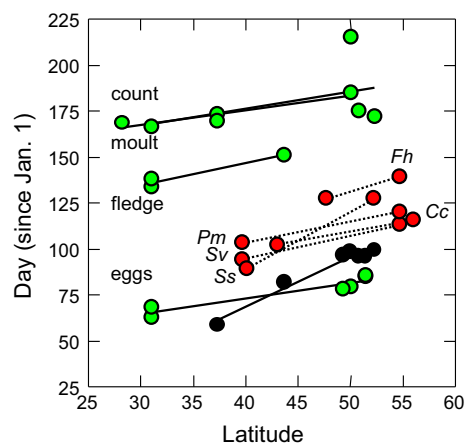

Fig. 3 Comparison of the timing of reproduction-related events (see text) as a function of latitude between the invasive Ring-necked parakeet (*green*) and timing of egg-laying of five European native species (*red*; Fh = *Ficedula hypoleuca*, Cc = *Cyanistes caeruleus*, Pm = *Parus major*, Sv = *Sturnus vulgaris*, Ss = *Serinus serinus*). Also plotted (*black*) is the estimated beginning of the growing season at all the sites for which we also have parakeet data, as based on standardized measures of tree phenology (see text)

Similarly, predictions of parakeet breeding phenology based on the development of woody vegetation across latitudes also results in later parakeet breeding dates than those actually observed in northern Europe (Fig. 3). According to the slope derived from tree phenology (2.69 days/°, N = 7, R^2 = 0.96, $F_{1,5}$ = 111.7, p = 0.00013, 95% CI 2.03–3.34 days/°), parakeets in northern Europe should breed about 65 days later (95% CI 49–81 days) instead of only 22 days as observed.

Discussion

Given the latitudes at which they occur, invasive Ring-necked parakeets breed earlier in Europe than in their native range (Fig. 2). Moreover, this difference is magnified towards northern Europe. Moving northward in Europe, we see a much stronger delay in breeding of invasive parakeets than in (1) parakeets in the native Indian range (Fig. 2), (2) native bird species in Europe (Fig. 3), and (3) the development of woody vegetation (Fig. 3). All these results support the hypothesis that the reproductive phenology of invasive Ring-necked parakeets can be a limiting factor for establishment and range expansion in colder climates.

Fig. 2 Timing of egg-laying by the Ring-necked parakeet in the invasive range (*black dots*, population averages) versus the native range (India, *grey dots*, individual clutches) as a function of latitude

Climatic conditions across parts of northern Europe where the parakeets are still absent may thus not necessarily be entirely unsuitable for Ring-necked parakeet establishment, but the parakeet's apparent failure to adapt their timing of breeding to the onset of spring may currently prevent this invader from establishing more northerly populations across Europe. The influence of such behavioral constraints on invasion success is difficult to predict from conventional niche modeling, because these often-used statistical techniques rely strongly on observed correlations between species presences and long-term climatic averages (Araújo and Peterson 2012) and assume that these correlations remain valid outside the native distribution. Instead, phenological mismatches can arise through the interaction between the seasonality of the area of introduction and the temporal niche of the invader. Since different traits such as adult resistance to low temperatures or reproductive timing may have different levels of phenotypic plasticity (within-generation responses to the environment) and evolutionary potential (between-generation responses to the environment), our results strongly suggest that the role of phenology in favoring or limiting biological invasions merits more attention than it currently receives.

Parakeet invasion and breeding success is lower in colder climates (Strubbe and Matthysen 2009a; Shwartz et al 2009), and the question thus remains why Ring-necked parakeets apparently fail to adapt their timing of breeding to prevailing environmental conditions in (northern) Europe. First, early breeding in Europe could be a strategy for avoiding intensive interspecific competition. Indeed, literature from the native (Asian) range suggests that parakeets may advance reproduction to avoid competition with more aggressive cavity-nesting species (Panicker 1980). In Israel early breeding helps parakeets outcompete the invasive Common myna (*Acridotheres tristis*), which is one of the main competitor for cavities in the native range of the two species (Shwartz et al. 2009; Orchan et al. 2013). However, this explanation is unlikely for Europe, since parakeets are considered to be superior competitors. For instance, it was found that parakeets were frequently initiating and mostly winning aggressive interactions with other species (Hernández-Brito et al. 2014), taking over nesting cavities (Strubbe and Matthysen 2009b), and possibly drive Starlings to breed later in the season (FERA 2010) and in

unpreferred cavities (Dodaro and Battista 2014) when cavities are more limiting.

Second, misinterpretation of environmental cues might also explain the early breeding in Europe. It is possible that parakeets base their breeding phenology decisions on cues that are adaptive in the native range, but fail in the invaded range. A common abiotic cue used for the timing of reproductive decisions by many species is the photoperiod, as it generally signals the changing of the seasons and the development of resources (Dawson et al. 2001). Another environmental factor which often influences reproductive timing is temperature, and accordingly many species reproduce earlier in relatively warmer years as a means to adjust to the resulting variation in the phenology of resources (Parmesan 2007). Maitra and Dey (1992) suggest that parakeets in India use the arrival of short day lengths to initiate their endogenous reproductive rhythm. It is conceivable that applying similar photoperiod-based cues in non-native Europe might result in a suboptimal timing of breeding, as the relationship between day length and development of (food) resources is likely to differ between Europe and India. The specific origin of the invaders might matter here (as e.g. in Edelaar et al. 2015), as adaptive timing to cues will often vary across species distribution ranges (Pearman et al. 2010).

Through genetic comparisons of mitochondrial haplotypes it has been established that the European Ring-necked parakeet populations originate almost exclusively (>99%) from Asian females (Jackson et al. 2015; Le Gros et al. 2016), even though up to 44% of all imported Ring-necked parakeets came from Africa (Cardador et al. 2016). This surprising lack of a clear African genetic signature (although nuclear loci suggest that African males seem to have been a bit more successful) has been explained by differences in climate matching (Jackson et al. 2015; Strubbe et al. 2015; Cardador et al. 2016). However, although a lack of detailed African data on breeding phenology prevented us from predicting timing of breeding for African parakeet clades, the literature (Cramp et al. 1994) mentions that many African populations breed from August to November. If this timing was maintained in Europe, this would result in a very poor timing of breeding (e.g. fledglings have to deal with declining food resources, day lengths and temperatures). That such mismatched timing might be maintained in the invasive range is indicated by a male African Ring-necked parakeet (*P. k. krameri*)

observed copulating with a female Alexandrine parakeet (*P. eupatria*) in August in Germany, when all other Asian Ring-necked parakeets were already in post-breeding state (Braun 2004). Such a clear mistiming of reproduction would virtually exclude the successful reproduction of African parakeets in Europe, even when the climate would generally be suitable. Finally, early breeding could be triggered by high food availability due to bird feeders and the presence of a diverse range of often early-flowering non-native ornamental plants in parks and gardens in its European invasive range. Radio-tracking studies found that invasive Ring-necked parakeets can strongly rely on such food resources, especially in winter and early spring (Clergeau and Vergnes 2011; Strubbe and Matthysen 2011; Franz and Dietzen 2016). Increased food availability is recognized as one of the main effects that humans exert on urban avian ecology (Robb et al. 2008; Oro et al. 2013) and it has been shown that anthropogenic food provisioning can allow birds to start the breeding season earlier (Verhulst and Nilsson 2008). In further support of this hypothesis, populations of the closely-related Mauritius parakeet (*Psittacula echo*) provided with supplementary food start breeding up to two weeks earlier than populations that are not given extra food (Simon Tollington pers. comm.).

How important is it if a parakeet population breeds a few weeks earlier than expected? The observed fitness consequences of mistiming have been large in native birds, with a mistiming of just a few weeks even associated with the near-extinction of local populations and the widespread decline of various species (Both et al. 2006, 2010). Similar effects should be expected for mistiming in invasive species too. Indeed, reproductive timing may also negatively impact upon European Ring-necked parakeets. First, it has been suggested that the high infertility of eggs in the United Kingdom—compared to Israel or the native range—is due to cold temperatures (Shwartz et al. 2009). Second, a roost count series from the German city of Wiesbaden suggests that yearly temperature fluctuations may underlie reduced parakeet invasion and breeding success, as years with a poor reproductive success (as judged by changes in maximum roost counts between years; Fig. 4) are characterized by markedly lower temperatures in the first half of the year. In further support of this, in several cities in Germany the species is increasingly using the thermal

insulation of walls of houses for breeding. The temperature in the cavities excavated in the insulation material is 2–4 °C higher than in natural tree cavities (Braun 2007), and fledging success seems higher for nests in insulation material (M. Braun, pers. comm.). Such observations support the idea that the parakeet is maladapted to the environment in the northern part of the invasive range as it decides to reproduce at a suboptimal moment in the year. Yet, the consequences of such mistiming may be at least partially offset in this particular species by its capacity to use a wide range of different food resources (including human-provided food), and its great behavioral flexibility and adaptiveness (including breeding in insulation material). Further improvement of reproductive success in the northern part of the invasive range could be expected as climates generally become warmer and spring becomes more advanced, reducing any effect of phenological mistiming.

In conclusion, our results contribute to the growing body of evidence supporting the underexplored hypothesis that the timing of important life history events such as reproduction can affect the establishment success, invasive potential and distribution ranges of non-native species. Taking this into account
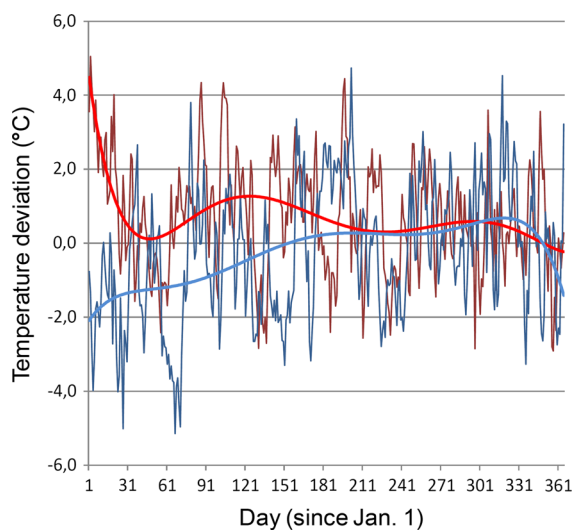

Fig. 4 In years with a larger population increase, temperature is higher in the first half of the year. Plotted are mean daily deviations from average temperature against date (and a smoothing line), for four good breeding years (*red lines*; 2003, 2005, 2007 and 2014) and three bad breeding years (*blue lines*; 2004, 2006 and 2010). (Weather data provided by the Weather Station of the University of Mainz, 1994–2014)

might help to understand and predict biological invasion success.

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