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Intra-specific variability in life-cycle synchronization of an ectoparasitic fly to its avian host

Miguel A. Calero-Torralbo, Radovan Václav and Francisco Valera

M. A. Calero-Torralbo (calero@eeza.csic.es) and F. Valera, Estación Experimental de Zonas Áridas (EEZA-CSIC) Ctra, Sacramento s/n, ES-04120 La Cañada de San Urbano, Almería, Spain. – R. Václav, Inst. of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84506 Bratislava, Slovakia.

The role of environmental and host-associated factors in synchronization of host–parasite life-cycles is an important question of evolutionary ecology. Yet, only handsome of studies examined this question at the intraspecific level. Here we explore how host-associated traits, such as breeding phenology and host breeding habitat, can influence parasite phenology and co-occurrence at different spatial scales. We studied the system comprised of a generalist ectoparasitic fly *Carnus hemapterus* and one of its avian hosts, the European roller *Coracias garrulus*. Inter-annual variation in phenology was larger for parasites than hosts. Host predictability in terms of occurrence and phenological regularity was moderate, suggesting that this resource can be difficult to be tracked by the parasite. A large proportion of flies consistently emerged before the appearance of suitable host resources at both the nest and population level. Consequently, we revealed low and highly variable inter-annual host–parasite synchronization rates. Nevertheless, we found that parasites from nests of early and progressively earlier breeding European rollers were more synchronized with their hosts than parasites from nests of late and progressively later breeding hosts, respectively. Temporal trends in host suitability and parasite emergence at the population scale suggest that other mechanisms, such as dispersal or exploitation of other host species, ensure parasites access to resources and counteract asynchrony with the host at the nest scale.

Understanding the dynamics of host–parasite interactions requires knowledge of the effects of environmental and host-related factors on the parasite's populations (Poulin 2007). Particularly, factors eliciting variation in host and parasite phenology can cause fluctuations of the parasite's prevalence and abundance in host populations (Godfray et al. 1994) and the level of host–parasite co-occurrence (Münster-Swedson and Nachman 1978).

For many parasites, phenological synchronization of their infective phases with the occurrence of sufficient resources is of vital importance to warrant the parasite's survival (Van Asch and Visser 2007). One main question is whether parasites can reliably detect or predict both the beginning and the end of the period during which resources are available. In fact, many parasites have evolved developmental and dispersal strategies (e.g. diapause) based on both host related and environmental external stimuli to counteract the risk of mis-synchronization their infective phase with the period when suitable hosts are available (Leather et al. 1993, Jones 2001, Poulin 2007, Krasnov 2008).

The degree of phenological host–parasite synchronization fluctuates widely due to multiple reasons such as differential sensitivity of each species to climate variation (heterotherms are more sensitive than endotherms to climate) or intraspecific variability in response to environmental factors. In herbivorous insects and parasitoids, wide intraspecific temporal and spatial variability in host–parasite co-occurrence has been reported within and among years due to variation in environmental factors such as temperature (Visser and Holleman 2001), photoperiod (Hegazi et al. 1988, Denlinger 2002), drought (Smith and Bronstein 1996), snowmelt (Høye and Forchhammer 2008), budburst or fruiting phenology (Van Dongen et al. 1997, Feder and Filchak 1999, Tikkanen and Julkunen-Tiito 2003, Teixeira and Polavarapu 2003). Moreover, the strength of host–parasite synchronization observed at a local scale can be modified by ecological forces constraining host or parasite population dynamics at regional scales (Van Nouhuys and Lei 2004). Therefore, it is important to consider spatial and temporal variation in phenological synchrony (Tikkanen and Julkunen-Tiitto 2003, Van Nouhuys and Lei 2004). Similarly, a deeper understanding of the effect of key ecological factors (e.g. photoperiod, temperature) and life-history traits of the host (e.g. host predictability, distribution or density) at different spatiotemporal levels is important, since fluctuations of these parameters can determine the optimal degree of host–parasite synchronization and the reproductive tactics of the parasite maximizing its fitness (Powell and Logan 2005, Barret et al. 2008, Krasnov 2008). Despite the importance of synchronization of host–parasite

life-cycles for the life-history strategies of 'true' parasites (i.e. parasites that usually do not kill their hosts) of animals (Hakalahti et al. 2004), variation and heterogeneity in host–parasite synchronization have been largely neglected and well-documented cases of host–parasite synchronization are scarce (but see Foster 1969, Larimore 1987, Rolff 2000, Randolph 2004).

The system involving the blood sucking ectoparasitic fly *Carnus hemapterus* and one of its avian hosts, the roller *Coracias garrulus*, provides an excellent opportunity to study host–parasite synchronization. First, *Carnus hemapterus* parasitizes ephemeral resources, namely, unfeathered nestlings of various bird species. Thus, adaptations to synchronize the parasite's life cycle with the breeding cycle of the host are expected. Indeed, the emergence of the parasite's infecting phases has been reported to be partly synchronized with the occurrence of their hosts (Liker et al. 2001, Valera et al. 2003, Calero-Torralbo and Valera 2008). Second, *Carnus hemapterus* can persist in the nest for several years (Valera et al. 2006a). Therefore, host nests can be viewed as discrete host entities, upon which fine-scale studies of host–parasite synchronization can be carried out. Moreover, information obtained at this level can be readily compared with that collected at larger scales (i.e. local patch or population levels). Third, temporal dispersal (by means of diapause) seems to be a major strategy for *Carnus* to synchronize its life cycle with the host (Valera et al. 2006a). Diapause is characterized by a high degree of plasticity and variability (Tauber et al. 1986, Danks 1987), so that diapausing parasites are ideal systems to study spatiotemporal variability of host–parasite co-occurrence. Fourth, breeding site fidelity has been reported for rollers (Václav et al. 2011), which can increase resource predictability for *Carnus* and, therefore, enhance host–parasite synchronization at both nest and local patch host levels. Fifth, in our study area rollers breed in different nest types with different microclimatic conditions and reproductive characteristics (Václav et al. 2011, Calero-Torralbo 2011), likely influencing host–parasite co-occurrence. Finally, roller is the latest breeding bird in our study area, setting the upper limit on seasonal parasite emergence.

Here we study host–parasite synchronization by examining host and parasite phenology during three years. We analyse the influence of host predictability and parasite phenological constancy on the co-occurrence of both species. We address the following hypotheses. First, environmental fluctuations can hinder host–parasite co-occurrence if their effects on both parasite and host phenologies are asymmetric (Van Nouhuys and Lei 2004). We predict that, in order to keep the high degree of host–parasite synchronization, inter-annual changes in environmental conditions should similarly affect the phenology of both hosts and parasites. Second, high host predictability can favour high parasite predictability (Barret et al. 2008). We predict that at the nest scale higher seasonal predictability of host breeding should be reflected by higher parasite inter-annual phenological regularity. Third, an accurate assessment of the period during which resources are available is vital for the parasite's diapause regulation. Such assessment is usually based on external factors, but also host-related life-story traits controlling the parasite's life-cycle regulation over parental or subsequent generations (Tauber at al. 1986). We therefore predict that host breeding phenology should be an important host trait used by the parasite to time its emergence.

Material and methods

Study area and species

The study area is located at the Desert of Tabernas (Almería, southeast Spain, 37°05′N, 2°21′W). The climate is semiarid with long hot summers and high annual and seasonal variability in rainfall (Lázaro et al. 2004) and significant both intra and interannual fluctuations of temperature (mean monthly oscillation temperature between 12.8 to 15.6°C, summer and winter coefficient of variation 8–11°C and 22–23°C respectively; Lázaro et al. 2001).

Carnus hemapterus (hereafter *Carnus*) is a 2 mm long blood-sucking fly that parasitizes unfeathered nestlings of a wide variety of species (Grimaldi 1997). Its life-cycle comprises an adult stage, three larval phases and a pupal phase (Guiguen et al. 1983). Usually, adult flies emerge in the spring after winter diapause when nestling hosts are available and emergence continues throughout the whole nestling period (Valera et al. 2003). Adult flies are initially winged, but typically lose their wings once they locate a suitable host (Roulin 1998). Carnid flies do not need a host for transmission and can colonise new host nests actively during the winged phase. Once emerged, adult *Carnus* cannot survive a long time without feeding (around 2–3 days; Calero-Torralbo unpubl.), and its dispersal period is short. Prolonged diapause has been recorded for this parasite, enabling *Carnus* to persist in the nest for several years (Valera et al. 2006a).

The European roller *Coracias garrulus* (hereafter roller) is a common avian host of *Carnus*. In our study area it breeds in burrows excavated by other birds in sandstone cliffs as well as in cavities in bridges. In addition, from 2005 we provided rollers with nest-boxes installed on trees and sandstone cliffs located near sandstone burrows and bridge cavities used by rollers (Václav et al. 2011). Microclimatic conditions vary widely among the nest types. Generally, within-day cavity temperature variation in bridge and sandstone cavities is small compared to that in nest-boxes. Cavities in bridges show higher humidity levels compared to sandstone burrows and nest-boxes (unpubl.). Nest cavities are usually reused by rollers but can also be used by kestrels *Falco tinnunculus*, jackdaws *Corvus monedula* or little owls *Athene noctua*. Rollers rear a single brood per year. Egg hatching is distinctly asynchronous with remarkable annual differences in hatching date as well as in clutch and brood size (Václav et al. 2008, 2011). Nestlings are naked at hatching, but, by the age of 13 days, their body is almost completely covered with closed feather sheaths. The sheaths open from around 15–17 days (Cramp 1985, Václav et al. 2008). Nestling rollers fledge approximately 20–22 days after hatching (Václav et al. 2008).

Data collection

(a) Host phenology

Fieldwork was carried out from 2005 to 2009. After sighting first roller copulations, potential nest cavities were inspected every other day until the day of hatching of the last chick of the study population. During regular nest inspections, we monitored and recorded egg laying, clutch size, hatching dates and nestling survival. In order to control the effect of host nest use on parasite population, we monitored host nest reoccupancy during the period 2005–2009. Hatching date of the first nestling of each brood was used as a measure of host phenology.

(b) Parasites phenology and abundance

The phenology of emergence of Carnid flies is not feasible to study in actively used nests due to logistic (rollers routinely expel alien material from their nests, including devices for trapping emerging flies) and ethical reasons (regular emergence monitoring would result in undesirable disturbance of host nestlings). Therefore, we studied the emergence of *Carnus* by monitoring subsamples of nest material stored under natural conditions (i.e. natural cavities or nest boxes in the study area). This method may underestimate the effect of roller incubation on diapausing pupae. However, Calero-Torralbo and Valera (2008) found that incubation by common avian host species did not result in significant changes in parasite phenology. *Carnus* emergence phenology was studied in 2006, 2007 and 2009. Substrate samples from the nest chamber of roller cavities used in the previous season (containing *Carnus* pupae from parental generation of the previous year and a low percentage of older pupae, Valera et al. 2006a) were collected during the beginning of March 2006, 2007 and mid November 2008 (34, 19 and 21 nests, respectively). After collection, samples were kept in transparent, not hermetically closed, plastic bags and stored in available cavities not used by overwintering or breeding birds. During 2006, samples collected from nests from sand cliffs and bridges were randomly assigned to the same or different cavity type, whereas samples collected from nest boxes were assigned to the other two nest types (i.e. natural and semi-natural cavities). In contrast, during 2007 and 2008 each sample was assigned to the same type of cavity from where it was collected, except for the samples collected from nest boxes during 2007, which were assigned to sand cliff burrows. To examine a potential effect of the cavity type on *Carnus* phenology, we compared the emergence pattern of samples stored in a cavity type different from the one where it was collected during 2006 and 2007 against the one involving samples obtained in 2009 when storage and origin cavity type were same. We explored differences at the beginning of the emergence (first quartile, 25% of emergence) when variability in the emergence is higher (Calero-Torralbo and Valera 2008). In 2006 and 2007 25% of flies from samples stored in a different cavity type emerged by the second and third week of May respectively, which was similar for samples kept in the same cavity type in 2009 when 25% of emergence was reached in the third week of May. Moreover, the emergence rate was similar regardless of the storage cavity type; GLMM, treatment fixed effect: $F_{1,93.16} = 0.03$, $p = 0.86$; nest identity random effect: $Z = 36.42$, $p < 0.001$; see below for statistical procedures.

Samples were regularly monitored (each 2–3 days) for emerged *Carnus* from 1 March 2006, 2007 and 2009 until 20 July in 2006, 10 July in 2007 and 5 July in 2009 (i.e. 10 days after the last fly was recorded). Parasite emergence was detected in 19 of 34 nests in 2006, 17 of 19 nests in 2007, and 20 of 21 nests in 2009 (parasite prevalence: 55.9%, 89.5%, and 95.2%, respectively). Emerged flies from each sample bag and during each inspection date were separately preserved in 99% ethanol and subsequently counted and identified with the aid of a binocular microscope.

Sample parasite emergence was defined by three variables: the weekly percentage of emerged flies, the length of emergence period (in days), and the date when 50% of *Carnus* flies emerged (in Julian days). We considered the date of 50% sample emergence as a reliable estimator of seasonal emergence progress for individual nests since most flies emerge around this date (Valera et al. 2006b, Calero-Torralbo and Valera 2008).

We also determined the sample's total abundance of flies, which was equal to the number of flies emerging in the nest sample, because the number of emerged flies was not clearly related to nest material weight (Spearman rank correlations for each year: $p > 0.1$, see also Valera et al. 2006b, Calero-Torralbo and Valera 2008).

(c) Host predictability and regularity of parasite emergence

We used two measures of host predictability and one of parasite emergence regularity:

a) Host occurrence: we calculated the rates of roller nest reuse between consecutive years and the lag between intermittent uses of roller cavities.
b) Phenology of host occurrence: since host breeding phenology may vary between years and nest types (Václav et al. 2011), host predictability was estimated by calculating the repeatability (following Lessells and Boag 1987) of the hatching date of the first nestling in different years for the same nest.
c) The regularity of parasite emergence was estimated by calculating the repeatability (following Lessells and Boag 1987) of the date when 50% of flies emerged in the same nest in different years.

(d) Host–parasite synchronization

The availability of suitable hosts for *Carnus* was calculated at the nest and population level considering the requirements and life cycle of the parasite. For rollers, the higher rates of *Carnus* infestation occur when the nestlings are unfeathered, quickly decreasing when feathers appear (about 14 days after hatching, Václav et al. 2008). Since *Carnus* can survive starving up to three days after its emergence, we extend the host availability period by three days before the first egg hatched in the respective nest. Although *Carnus* flies can feed on the brood patch of incubating adult birds (Calero-Torralbo et al. unpubl.; see also López-Rull et al. 2007, Avilés et al. 2009), adult birds are

an apparently suboptimal and unsafe food source compared with nestlings. For example, adult birds can kill flies by preening or drop them from body accidentally outside of the nest. Also, adult immune system is capable to greatly reduce feeding efficiency of hematophagous parasites compared to juvenile hosts (Liberman et al. 2011). Lastly, *Carnus* feeding on adults likely occurs mainly around the date near egg hatching when incubation is most intensive. Therefore, we determined the optimal host availability period to last 18 days from day −3 to day +14, with day 0 being the date when the first egg hatched and day 14 being the date when the earliest nestling becomes feathered. The period of host availability can increase depending on the number of nestlings in the nest as hatching is asynchronous in rollers. We therefore extended the period of host availability according to the number of nestlings in the brood. Consequently, the period of host availability ranged from 18 days (one nestling broods) to 28 days (six nestlings broods).

We calculated an index of host–parasite synchronization at the nest level as follows: we measured the percentage of flies emerging during the period of 18 days when the most suitable hosts are available. This index is conservative because only the first hatched chick per nest was considered and host brood size did not affect it. The synchronization index requires that data of host hatching dates and parasites emergence dates are available for the same nest during the same year. Since Rollers do not always occupy the same nest in consecutive years (or breeding may fail), it was not possible to calculate the synchronization index for all samples. As a result, the sample size for the synchronization index (n = 40 nests: 14 in 2006, 11 in 2007, and 15 in 2009) was lower compared with the number of nests with emerged parasites (n = 56) and successful host breeding attempts (n = 195).

Statistical analyses

To test the effect on the emergence rate of translocation of nest box samples to other cavity types (see section (b) of Material and methods), we used generalized linear mixed model (GLMM), with binomial distribution error. The number of emerged flies during one week interval divided by the number of all emerged flies was used as a response variable. To account for the repeated measures effect (11 emergence observations for each nest sample), we used the repeated measures design and the first order autoregressive, AR(1), covariance structure (Littell et al. 2006). Hereby, the sampling period was considered as a time measure (with one week intervals) and the sample's nest identity was used as a subject unit.

We evaluated niche variation in host and parasite phenology by analysing intra-annual differences among nest types and inter-annual differences in host hatching date, the length of parasite emergence and the date when 50% of *Carnus* flies emerged. We analysed inter-annual and cavity type differences also for parasite abundance. After checking the assumptions of parameterization, we performed general linear mixed models (GLM) with normal distribution, except for parasite abundance, for which we used a Poisson distribution and GLMM. Year and nest identity were analysed as repeated measures data including the AR(1) covariance structure; year and cavity type were analysed as fixed effects. We performed post hoc tests of significance when opportune. Three of 56 nests were discarded for the analysis of parasite phenology due to the low (less than five individuals) and clumped emergence of flies.

We also analysed the effect of year and cavity type on the percentage of host–parasite synchronization by performing GLM with normal distribution. Year and nest identity were included as a repeated measures effect with the AR(1) covariance structure, and year and cavity type as fixed effects. We conducted post-hoc tests of significance when opportune. Additionally, to test the effect of host breeding phenology on host–parasite synchronization in a given year (year t), we recorded previous (year $t-1$) and current (year t) host-hatching dates for nests where parasite emergence was recorded during year t. GLMs with normal distribution were performed, including year and nest identity as a repeated measures effect, and year and either host hatching date in year t or the difference in host hatching date between year t and $t-1$, $\Delta(t-(t-1))$, as fixed effects.

Results

Host phenology, predictability and nest reuse

Host hatching period at the population level (i.e. the period between the date of hatching of the first nestling in the earliest nest until the date of hatching of the first nestling in the latest nest) spanned from the fourth week of May until the fourth week of June for 2005–2008 and from mid May until mid July for 2009 (Fig. 1). The mean length of the suitable host period during the five years study was 53.4 days (see Table 1b for additional information).

At the nest level, the mean period of suitable host availability was 22.63 days (SE = 0.14; n = 195). Host hatching dates did not differ among years during 2005–2009, but we observed significant differences among nest types (GLM, repeated measures effect: year with nest ID as a subject, $Z = 5.103$, $p < 0.001$; fixed effects: year, $F_{4,105.2} = 1.93$, $p = 0.111$; cavity type, $F_{2,103.5} = 4.76$, $p = 0.010$; year × cavity type, $F_{8,109.6} = 0.86$, $p = 0.555$). Hosts hatched significantly earlier in nest-boxes (nb) than in bridges (b) and tended to hatch earlier in nest-boxes than in sandstone burrows (s) (post hoc tests; b. vs nb. $t_{107.9} = 3.07$, Sidak-adjusted $p = 0.008$; s. vs nb. $t_{116.6} = 1.69$, Sidak-adj. $p = 0.065$; s. vs b. $t_{92.24} = 5.97$, Sidak-adj. $p = 0.69$).

Host predictability varied among years. The repeatability of host hatching dates in different years for the same nests during the whole study period was 0.26 (Table 2). However, repeatability varied widely depending on the time lags between different years, ranging from no repeatability for some years to a maximum of 0.70 for the three-year period of 2007 to 2009 (Table 2).

The rate of nest reoccupancy in our area was not high. Monitoring nest cavities (all types) during the period 2005–2009 showed that approximately a half (53.3%; 56/105) of them were used only once by the host,

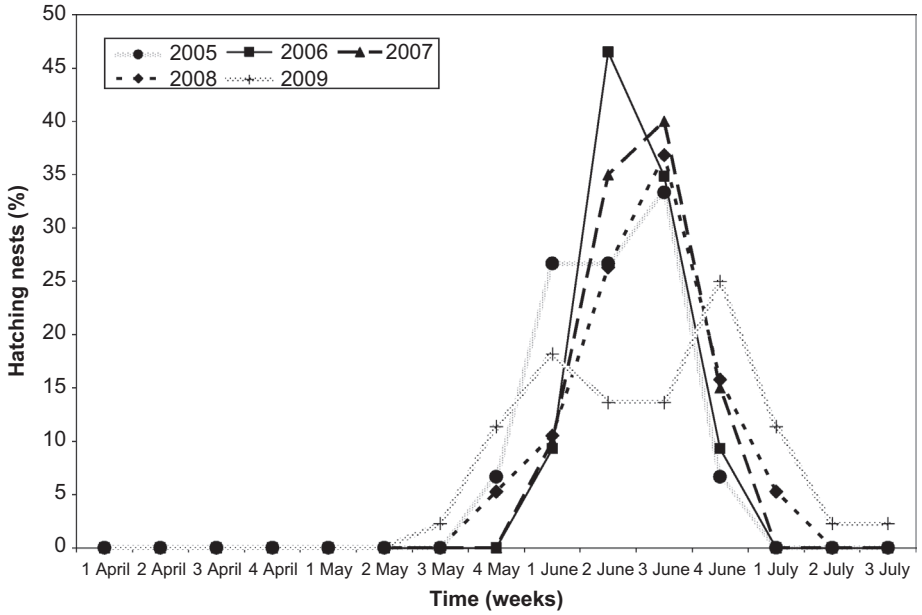

Figure 1. Seasonal trend in the percentage of roller nests with first-hatched nestlings during five seasons (n = 30, 43, 40, 38 and 44 nests in 2005, 2006, 2007, 2008 and 2009, respectively).

24 (22.8%) were used two times, 15 (14.3%) were used three times, four cavities (3.8%) were used four times and six (5.7%) were used five times. Approximately a half of the nests used more than once were used intermittently: 50.0% (9/18) bridge cavities, 50.0% (7/14) sandstone burrows, and 29.4% (5/17) nest-boxes. The lag between two nearest breeding attempts was one to three years (lags, one year: 16; two years: 3; three years: 2).

Table 1. (a) Host hatching phenology (hatching date of the first nestling in the earliest and latest nest) and (b) dates of length of host availability and parasite emergence at the population level, during the five years of study (2005–2009). Hatching dates and the date of parasite emergence are measured in Julian calendar days.

(a)

Year	Range	Minimum and maximum	n	Mean	Median	Skewness
2005	27	145–171	30	158.3	158.5	−0.1145
2006	25	151–175	43	161.3	160.0	0.3415
2007	25	151– 175	40	162.4	162.0	0.1890
2008	38	143–180	38	162.3	162.5	−0.2199
2009	60	134–193	44	165.0	165.0	−0.0767
2005 to 2009	60	134–193	195	161.7	162.0	0.1103

(b)

	Host availability			Parasite emergence		
Year	Earliest date	Latest date	Range	First fly	Last fly	Range
2005	142	189	48	–	–	–
2006	148	193	46	100	180	81
2007	148	193	46	109	184	76
2008	140	195	56	–	–	–
2009	131	201	71	97	176	80
2005–2009	131	201	71	–	–	–
2006–2007–2009	–	–	–	97	184	86

Phenology of parasite emergence and interannual regularity

The parasite's emergence period at the population level (i.e. the period between the date of the emergence of the earliest fly until the date of the latest fly) spanned from the second week of April until the first week of July for 2006, from the third week of April until first week of July for 2007, and from the second week of April until the fourth week of June in 2009 (Fig. 2). The mean length of the period of three years was 79 days (Table 1b for additional information). For 75% of samples where flies emerged, emergence started before the first week of June when host hatching was extensive during the three years. Parasite emergence progressively increased along the season, with a sudden decrease after the peak was reached (Fig. 2), as evidenced by the negative skew of the distribution of parasite emergence for all three years (skewness: 2006 = −0.556, 2007 = −0.730, 2009 = −0.568). In contrast, at the nest scale the number of flies quickly increased, remaining relatively stable during the first four weeks of emergence and decreased progressively thereafter (Fig. 3).

At the nest level, the length of the emergence period (the date of emergence of the first fly until the date of emergence of the last fly for the same nest) averaged 38.5 days during three study years (2006: mean = 41.3 days, SE = 6.65, n = 16; 2007: mean = 37.2 days, SE = 3.51, n = 17; 2009: mean = 37.4 days, SE = 2.84, n = 20) and differed between years and cavity types (GLM, repeated measures effect: year with nest ID as a subject, Z = −1.99, p = 0.0466; fixed effects: year $F_{2,40.91} = 5.58$, $p < 0.01$; cavity type: $F_{2,26.59} = 13.64$, $p < 0.001$; year × cavity type: $F_{4,42.06} = 5.18$, $p < 0.01$). However, as the interaction term year × cavity type suggests, these differences were only produced by the differences in the length of the parasite's emergence period in nest-boxes during 2006, but not during 2007 and 2009 (post hoc tests;

Table 2. Host and parasite repeatability for different periods (inter-annual differences in hatching dates of first-hatched nestlings in the same nest and inter-annual differences of the date when 50% of flies emerged in the same nest, respectively). The number of years examined is showed in parentheses and significant values are in bold.

Host				Parasite			
Years	Repeatability	p	n	Years	Repeatability	p	n
2005 to 2009 (5)	**0.26**	0.040	6	2006–2007–2009 (3)	0.38	0.080	5
2006 to 2009 (4)	**0.48**	0.006	6	2006–2007 (2)	**0.57**	0.029	10
2005 to 2008 (4)	0.16	0.177	6	2007–2009 (2)	**0.64**	0.030	7
2005 to 2007 (3)	−0.14	0.745	9				
2006 to 2008 (3)	0.46	0.167	8				
2007 to 2009 (3)	**0.70**	>0.001	13				
2005 and 2006 (2)	0.06	0.410	16				
2006 and 2007 (2)	0.18	0.234	18				
2007 and 2008 (2)	**0.60**	0.004	16				
2008 and 2009 (2)	**0.62**	>0.001	22				

b. vs nb., $t_{36.02} = -5.07$, Sidak-adjusted $p < 0.001$; s. vs nb., $t_{26.98} = 4.14$, Sidak-adj. $p = 0.009$; s. vs b. $t_{26.79} = -1.09$, Sidak-adj. $p = 0.63$; 2006 vs 2007, $t_{39.07} = 2.55$, Sidak-adj. $p = 0.043$; 2006 vs 2009, $t_{40.63} = 3.25$, Sidak-adj. $p = 0.007$; 2007 vs 2009, $t_{39.63} = 0.30$, Sidak-adj. $p = 0.99$).

Parasite phenology (the date when 50% of parasites emerged) differed between years and cavity types (GLM, repeated measures effect: year with nest ID as a subject, $Z = 3.08$, $p < 0.01$; fixed effects: year $F_{2,25.18} = 12.93$, $p < 0.001$; cavity type: $F_{2,34.78} = 22.94$, $p < 0.001$; year × cavity type: $F_{4,26.18} = 1.45$, $p = 0.25$). Fifty per cent of emergence occurred earlier in nest boxes compared with sandstone burrows and bridge cavities (post hoc tests; b. vs nb., $t_{36.02} = 6.39$, Sidak-adjusted $p < 0.001$; s. vs nb., $t_{36.24} = -5.62$, Sidak-adj. $p < 0.001$; s. vs b., $t_{32.49} = 5.97$, Sidak-adj. $p = 0.70$) and occurred later in 2007 than in 2006 and 2009 (post hoc tests; 2006 vs 2007: $t_{20.9} = -3.68$, Sidak-adjusted $p = 0.003$; 2006 vs 2009: $t_{37.54} = 0.46$, Sidak-adjusted $p = 0.96$; 2007 vs 2009 $t_{30.57} = 4.45$, Sidak-adjusted $p < 0.001$). Parasite phenology within the same nests was repeatable between 2006 and 2007, 2007 and 2009, and tended to be repeatable among the three study years (2006, 2007 and 2009; Table 2).

Determinants of parasite abundance

Carnus abundance (i.e. the number of flies emerged from nest samples) did not differ significantly between years (GLMM, repeated measures effect: year with nest ID as a subject, $Z = 4.51$, $p < 0.001$; fixed effect: year, $F_{2,42.91} = 1.20$, $p = 0.31$). However, it did differ between cavity types (cavity type, $F_{2,42.97} = 6.36$, $p = 0.004$; year × cavity type, $F_{2,43.07} = 0.62$, $p = 0.65$) due to the higher abundance for nest-box samples compared to the samples from bridge cavities (nb. vs b. $t_{42.7} = -3.55$, Sidak-adjusted $p = 0.028$) and the marginally higher abundance for nest-box compared with sandstone samples (nb. vs s. $t_{42.15} = 2.30$, Sidak-adjusted $p = 0.062$).

Host–parasite synchronization

At the population level the mean length of the fly emergence period was 1.48 times longer than the mean length of the suitable host period (79 vs 53.4 days). At the nest level the period of fly emergence was significantly longer than the period of suitable host availability (38.5 vs 22.6 days) (1.70 times longer, *t*-test for dependent samples $t_{52} = -6.16$, $p < 0.001$, data coming from

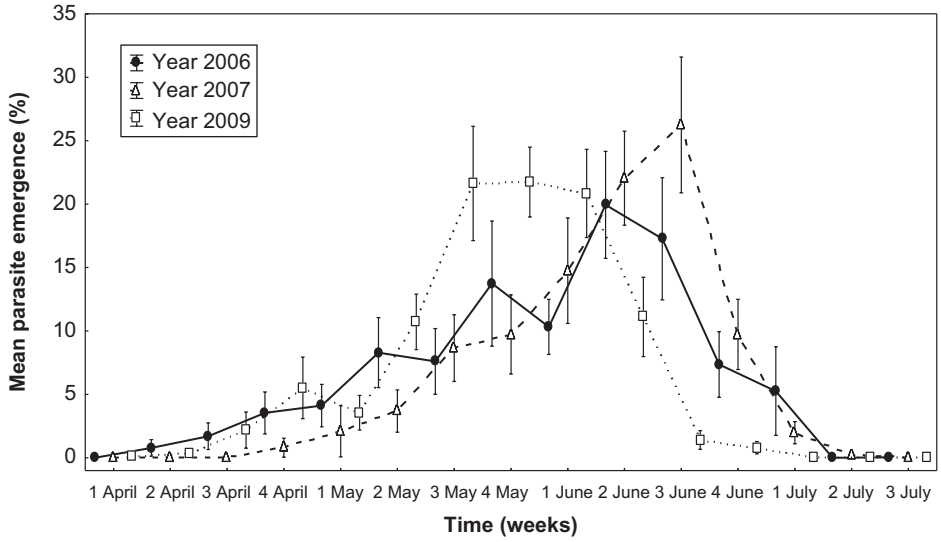

Figure 2. Seasonal trend in mean (± SE) percentage of parasite emergence for years 2006, 2007 and 2009 and n = 19, 17 and 20 nests, respectively.

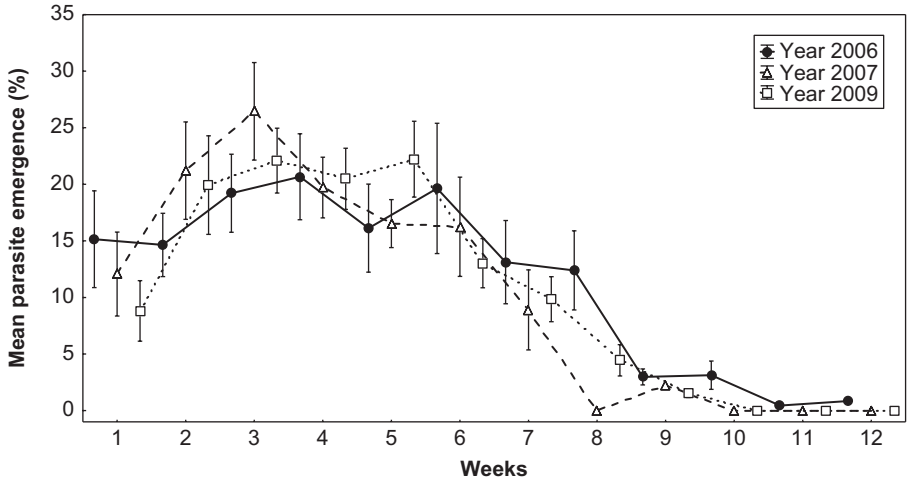

Figure 3. Temporal trend in mean (± SE) percentage of parasite emergence (n = 19, 17 and 20 nests in 2006, 2007 and 2009, respectively). Since the start of emergence varied among nests and years, data were organized so that week 1 represents the start of the emergence regardless of the actual parasite emergence date.

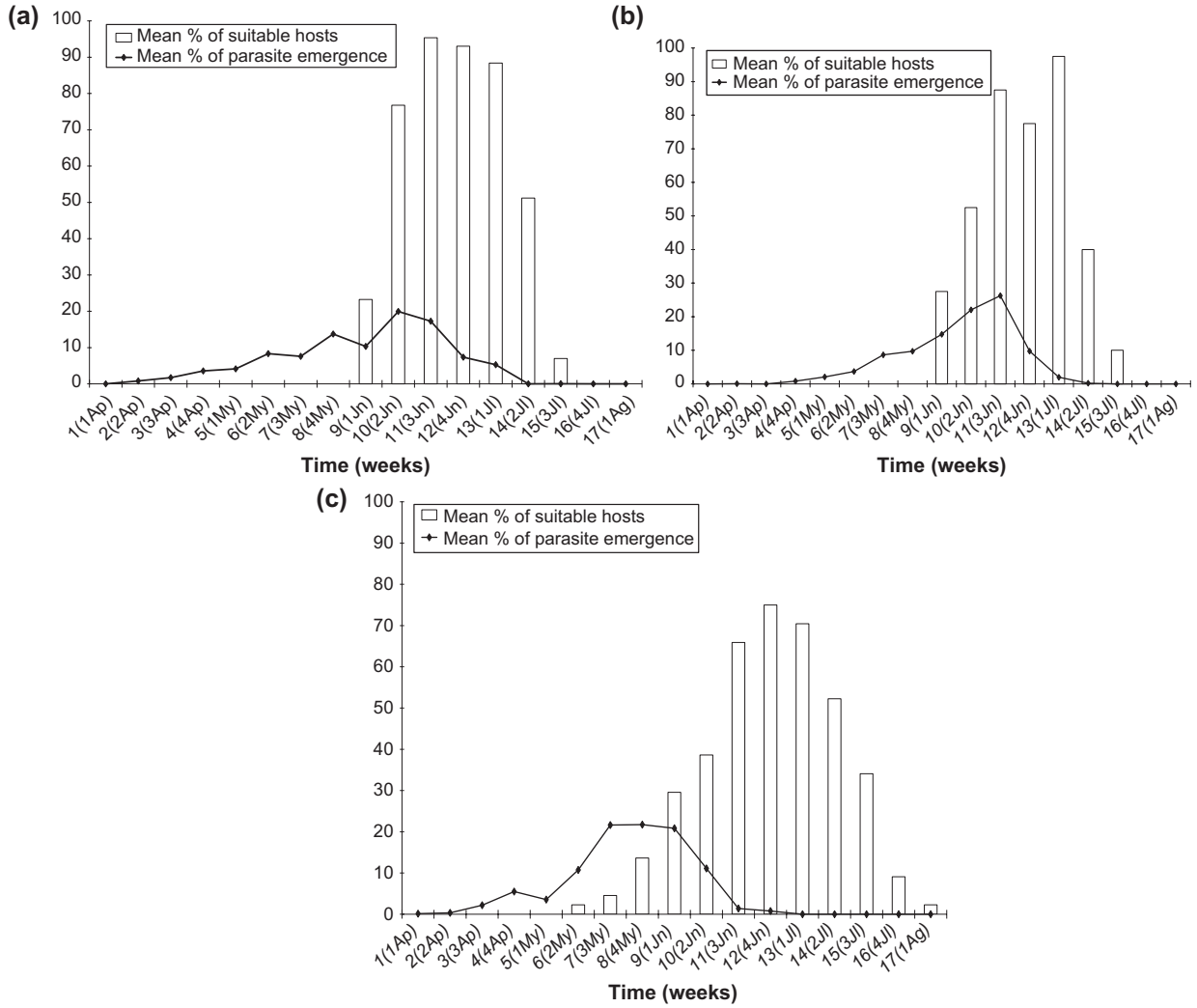

Figure 4. Host–parasite phenology co-occurrence for years (a) 2006, (b) 2007 and (c) 2009. All nest type data are pooled for every year. Bars show the mean weekly percentage of suitable nestlings of the roller population. Lines show the mean weekly percentage of parasite emergence. Host sample sizes (nests): 2006 = 43; 2007 = 40; 2009 = 44. Parasite sample sizes (sampled nests): 2006 = 16; 2007 = 17; 2009 = 20.

nests where both fly emergence and host suitability was recorded). Consequently, some flies emerged in each year when no suitable roller host was available (Fig. 4a–c). This mismatch affected the earliest flies so that, on average, one quarter of the studied population emerged before the occurrence of the earliest host (2006: 39.8%, 2007: 25.0% and 2009: 11.7%; Fig. 4).

Host–parasite synchronization at the nest level was highly variable (Table 3) and differed among years, but not among cavity types (GLMM, repeated measures effect: year with nest ID as a subject, $Z = 0.10$, $p = 0.92$; fixed effects: year, $F_{2,31} = 8.70$, $p = 0.001$; cavity type, $F_{2,31} = 1.08$, $p = 0.35$; year × cavity type, $F_{4,27.49} = 2.52$, $p = 0.064$). The year effect was related to the lower host–parasite synchrony in 2009 compared with 2006 and 2007 (post hoc tests; 2006 vs 2007, $t_{22.97} = -0.03$, Sidak-adjusted $p = 1.000$; 2006 vs 2009, $t_{31} = 3.73$, Sidak-adj. $p = 0.0023$; 2007 vs 2009, $t_{31} = 3.92$, Sidak-adj. $p = 0.0014$; Table 3).

Regardless of nest identity, host–parasite synchronization was influenced by host hatching dates (GLM, repeated measures effect: year with nest ID as a subject, $Z = 3.36$, $p < 0.001$; fixed effects: year $F_{2,36} = 16.95$, $p < 0.001$; host hatching date, $F_{1,36} = 14.88$, $p < 0.001$), with synchronization increasing with decreasing host hatching dates (Fig. 5a). When accounting for nest identity, an accelerated breeding of the host in year t relative to year $t-1$ resulted in a higher degree of host–parasite synchronization in t (GLM, repeated measures effect: year with nest ID as a subject, $Z = 3.45$, $p < 0.001$; fixed effects: year $F_{2,36} = 16.40$, $p < 0.001$; Δ host hatching date between year t and $t-1$, $F_{1,36} = 8.94$, $p = 0.005$; Fig. 5b).

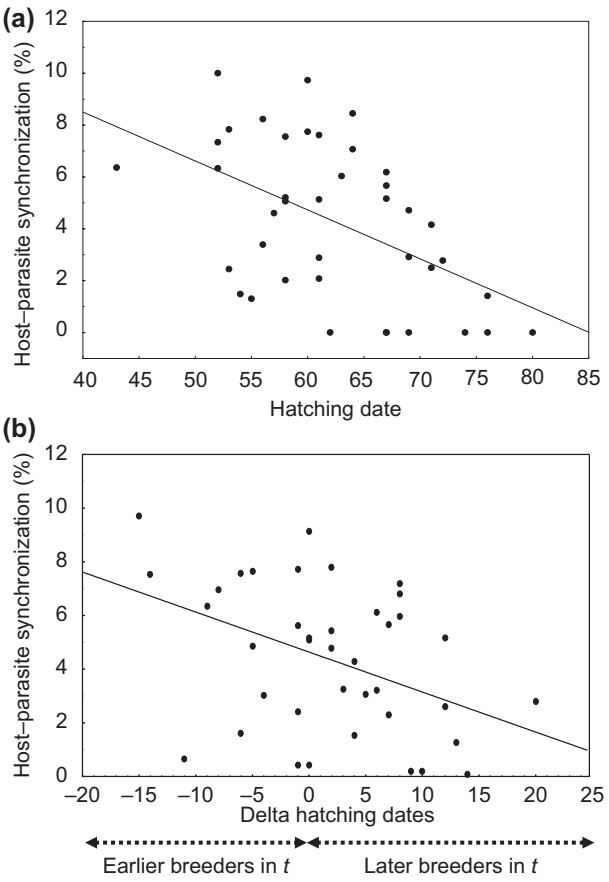

Figure 5. Relationship between (a) host hatching date (in Julian days) and the degree of host–parasite synchronization in year t and (b) between the change in host hatching dates between year t and year $t-1$ and the degree of host–parasite synchronization in year t. The change in hatching dates was obtained by subtracting the date of hatching of the first nestling in year t (in Julian days) from the hatching date of the first nestling in year $t-1$. Percentage values of host–parasite synchronization in both figures were square-root transformed to ensure normality.

Discussion

Comparison of host and parasite phenologies and parasite abundance

Our study revealed some similarities and differences in the phenology of the studied host–parasite system. At the population level, the mean *Carnus* emergence period was 1.48 times longer than the average length of the suitable host period, with parasites emerging consistently several weeks earlier than the majority of host nestlings. The shape of the distribution of host hatching dates varied among years, but the mean skew was positive for the five years of study. In contrast, the distribution of *Carnus* emergence showed a strong, consistent negative skew, likely reflecting the lack of suitable hosts at the end of the breeding season (see also Fargallo et al. 2001, Martín-Vivaldi et al. 2006, Calero-Torralbo and Valera 2008 for similar results).

Table 3. Mean percentage of host–parasite synchrony, i.e. % of flies emerging during the period when most suitable hosts are available, per year and cavity-type. Sample sizes are showed in parentheses.

	Nest cavities			
Year	Sand cliffs	Bridges	Nest-boxes	Total
2006	49.55 (5)	55.26 (7)	4.21 (2)	45.93 (14)
2007	30.70 (4)	14.96 (2)	32.76 (5)	28.78 (11)
2009	1.25 (5)	15.87 (4)	10.31 (6)	8.78 (15)
Total	26.92 (14)	36.95 (13)	18.01 (13)	27.28 (40)

The observed distribution of *Carnus* emergence can be the result of the coexistence of various parasite cohorts. The presence of cohorts of different parental genotypes may produce different Genotype × Environmental interactions (i.e. genotypes with different or limited thermal sensitiveness, Kemp and Bosch 2005). A population mixture of roller-associated univoltine flies with bivoltine generations coming from flies parasitizing earlier hosts (such as regional *Leptidea* butterflies populations coming from different habitats, Friberg et al. 2008), or one-year life-cycle flies versus longer-than-one year life-cycle flies (prolonged diapause, Valera et al. 2006a) would produce a wide emergence window. Nonetheless, regardless the functional origin of the observed distribution, from an evolutionary point of view, early emergence of a particular fraction of the parasite population might be an effective strategy for flies exploiting late host breeders, since earlier flies emerging from late host species can infect early host species of the local avian community. Alternatively, earlier phenotypes emerging in late host species might reduce the chance of complete or partial parasite reproductive failure

if host reproduction fails in the nest of parasite origin (Wiklund and Friberg 2004). Interestingly, the seasonal pattern of *Carnus* emergence can differ between species (Valera et al. 2006a, Calero-Torralbo and Valera 2008, Calero-Torralbo 2011), suggesting that hosts' species phenologies can shape life-cycles of associated parasite populations (Feder and Filchak 1999, Tabuchi and Amano 2003).

Our results show that at the nest level the emergence period of the parasite was also longer (1.7×) than the period of suitable host occurrence. Even though the occurrence of different cohorts could explain the long and variable emergence period, some synchronization between host availability and parasite emergence seemed to have occurred at the nest level. The most remarkable feature in this regard was the rapid increase in *Carnus* emergence at the beginning of the host breeding season, with more than 50% of flies emerging in the first four weeks. This high emergence rate at the beginning of the emergence period suggests that flies emerging from the nest substrate try to synchronize their occurrence with the early nestling period when nestlings Rollers are unfeathered (Václav et al. 2008). A positively skewed emergence is common in insects (Danks 2006) since most individuals usually respond rapidly and similarly to relevant environmental cues. Knowledge about environmental factors used by *Carnus* to emerge is still incomplete, although ambient temperature combined with host-related cues has been suggested to play the main role in a rapid *Carnus* emergence and diapause arrest at the nest level (Calero-Torralbo and Valera 2008, see also Tauber et al. 1986, Leather et al. 1993 for other systems).

Roller and *Carnus* phenologies were comparably influenced by some factors but not by others. Inter-annual variation in roller hatching dates was minimal and slight inter-annual differences in skewness likely reflects certain plasticity in hatching dates distribution around a stable population mean. In contrast, parasite phenology (50% emergence and the length of the emergence period) was more sensitive than host phenology to inter-annual changes. This is feasible because temperature is known to have a profound impact on growth and emergence patterns of heterothermic invertebrates (Tauber et al. 1986). On the contrary, for endotherm organisms, a direct effect of environmental temperature on breeding phenology is weaker and temperature is generally only used as a cue to the occurrence of the most favourable period for reproduction (Visser et al. 2009, Forrest and Miller-Rushing 2010). Therefore, our study implies that the annual fluctuations of environmental variables can produce different effects on host and parasite phenologies and thus alter the degree of mismatch over host–parasite co-occurrence (see also Van Nouhuys and Lei 2004). In contrast, nest type had a similar effect on the host and the parasite: both the roller and carnid flies advanced their life cycle (hatching date and emergence, respectively) in nest-boxes. Different microclimate conditions when compared with natural cavities can account for these effects, even though earlier breeding of rollers in nest boxes could also be caused by intra- or inter-specific host competition for nest sites (Václav et al. 2011). Nest boxes also affected host–parasite relationships via parasite abundance. Flies were more abundant in nest boxes than in the other nest types (Møller 1989, Fargallo et al. 2001, Wesolowski and Stanska 2001), probably due to microclimate and nest substrate composition, affecting different stages of the parasite (Dawson et al. 2005, Krasnov 2008, Martínez-de la Puente et al. 2010), or difficulties in nest sanitation by the host. Albeit the use of nest-boxes in the study of the ecology of hole-breeding birds is widespread, our results suggest caution when extracting conclusions from phenological studies involving endothermic organisms and ectothermic species such as avian ectoparasites.

Host predictability and parasite phenological regularity

High host predictability across years is vital to promote parasite predictability and host–parasite synchronization (Barrett et al. 2008). Host predictability fluctuated in our study system: 1) host occurrence was moderate, with some nests being used only once and others being used consistently for several years; 2) inter-annual hatching date repeatability for the same nest was highly variable, ranging from no repeatability for some years to 0.70 for a three-years period. In contrast, parasite phenological predictability for the same nest was less variable during the study period (Table 2).

Differences between host and parasite predictability are probably reflecting the different nature of the factors influencing phenology in each organism. *Carnus* emergence is highly dependent on diapause duration, which is rather rigidly regulated by ambient temperature (Calero-Torralbo and Valera 2008, Valera et al. unpubl.). Unless a major environmental disturbance occurs, a given nest is likely to maintain its thermal characteristics between years. In contrast, host phenology in a given nest can be influenced by a variety of biotic factors that are difficult to predict (but see Pryzbylo et al. 2000). Václav et al. (2011) showed for the same host population that Roller nest reoccupancy was more likely if the nest had been previously used, although this effect was only detected for natural cavities and traditional nests in human constructions. Thus, although host predictability could be hardly forecasted by *Carnus* at the host population level, opportunities for a relatively high synchrony do exist for some nests that are occupied consistently and with a high phenological predictability by the same host (cf. Van Dongen et al. 1997, Tikkanen et al. 2006).

Host–parasite synchrony

In host–parasite interactions synchrony occurs when the life cycle of the parasite is timed so that it can exploit the host optimally and that of the host is timed to be maximally exploited (Singer and Parmesan 2010). Our data show that, at the nest level, host–parasite synchronization was low (Table 3), mainly because *Carnus* consistently emerged before the occurrence of the host. This indicates that flies cannot precisely detect or predict the beginning of the period of host availability (Buse and Good 1996). The question appears to what extent *Carnus* can track the phenology of rollers.

Host–parasite synchronization was tightly linked to host breeding phenology. First, more advanced host breeding resulted in a higher degree of synchronization. Second,

more accelerated host breeding between consecutive years also resulted in higher host–parasite synchronization. Consequently, birds initiating their breeding earlier, both in terms of absolute and relative hatching dates, faced a higher parasitism risk than later and progressively delayed host breeders.

The level of host–parasite asynchrony detected in our study raises the question of whether perfect synchronization with their roller hosts is indeed the optimal strategy for *Carnus* to maximize its fitness or, on the contrary, a certain degree of stochasticity is desirable to face host unpredictability and/or take advantage of alternative resources. If individuals can precisely detect when resources are available, then a population of parasites could develop an ideal strategy of close co-occurrence and synchronization (Singer and Parmesan 2010). In turn, in the absence of predictable cues and/or conditions, parasite generalists tend to show a broader phenology in an attempt to encompass a broader phenological window at the community level (Tikkanen and Lyytikäinen-Saarenmaa 2002). Recent work suggests that some stochastically regulated life-history strategies, entailing some degree of host–parasite asynchrony and parasite extended phenology (e.g. bet-hedging, coin flipping and other stochastically regulated strategies), can be an efficient response toward the low predictability and extreme irregularity of the hosts (West-Eberhard 2003). Our results support this affirmation (cf. Pasternak et al. 2000, Fenton and Hudson 2002, Crossan et al. 2007). Importantly, negative consequences of such strategies could be partially offset by the acquisition of host searching skills during the dispersal period (Combes 2001).

In our system, host–parasite synchronization at the nest level reached 8.78% in 2009. Yet, 88.3% of all flies emerged during the period of suitable host availability in 2009. This suggests that stronger selection for parasite synchronization could operate at the population or community level (cf. Jepsen et al. 2009) compared to that at a fine, nest level. Additionally, massive and rapid colonization of isolated new nest-boxes by carnid flies (Calero-Torralbo unpubl.) suggests that winged adults are equipped with efficient searching skills to detect occupied nests.

Our study suggests that low host–parasite synchronization may be advantageous in the parasitic system facing a high degree of host and environmental unpredictability at fine spatial and temporal scales, lending the support to the hypothesis of the evolutionary significance of phenological asynchrony (Singer and Parmesan 2010).

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