

# Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor

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**Abstract** No environment is truly constant in time. As a result, animals have evolved multiple adjustments to cope with such fluctuations. However, the allocation of effort to costly activities that imply long-term commitments, such as breeding, may be extremely challenging when future resources change constantly and unpredictably, a context that has received little investigation. To fill this gap, we studied the breeding response by a wetland-dependent raptor, the black kite *Milvus migrans*, to within and between-years fluctuations in resource availability (inundation levels). The breeding performance of the population was decomposed into reproductive components expressed in a sequence of successive tasks along the breeding cycle (e.g. timing of laying, clutch size, hatching success, brood reduction). Variation in each component was related to resource levels observed at different key dates of the season in order to test whether and when population-level reproduction was adjusted to available resources. Along a 22-year time-series, inundation levels fluctuated unpredictably within and among years, and mostly affected the later components of kites' reproduction, such as hatching

success and the incidence of brood reduction, which were the main determinants of the population yearly breeding output. Results were consistent with multiple adjustments to cope with uncertainty. As the season progressed and resources became easier to assess, a bet-hedging waiting strategy based on a conservatively small, invariant and asynchronous clutch gave way to real-time resource-tracking mechanisms mediated by progressive adjustments to current prey availability, so that population-level breeding rates were determined and tuned to resources rather late in the season. Such adjustments were the likely outcome of the interaction between parental tactics and environmental constraints. Behavioural flexibility, such as dietary opportunism, probably promoted further resistance to resource oscillations. Given that all ecosystems show some degree of unpredictability, resource-tracking adjustments, such as the ones depicted here, are likely to be commonplace in most communities.

**Keywords** Brood reduction · Environmental uncertainty · Hydrology · Inundation-rates · Resource fluctuations · Water-levels

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## Introduction

No free-living organism experiences a truly constant environment, especially if it lives more than 1 year, as do most vertebrates (Wingfield 2008). As a result, most animals have evolved strategies to cope with such fluctuations (e.g. Winne et al. 2006; Shine and Brown 2008), especially when these coincide with costly life-history stages, such as reproduction. Breeding is an important component of fitness that imposes high energetic demands and thus needs to be fine-tuned on available resources in order to avoid

excessive fitness costs to both parents and offspring (Thomas et al. 2001). In seasonal environments, organisms are usually thought to plan their reproductive effort by integrating two types of information: (1) signals that allow them to make long-term predictions about the state of the environment in the future, such as day-length and photoperiod (“initial predictive information”; Wingfield 2008); (2) shorter term cues, such as food abundance or rainfall, that allow them to fine-tune the above information on available resources (“local predictive information”; Wingfield 2008).

An especially challenging scenario for reproductive planning is represented by environments in which resource availability changes constantly during the breeding season and is dependent on extreme disturbances, such as drought, or other unpredictable factors, such as rainfall in arid regions. Such unpredictable fluctuations are powerful drivers of life-history traits (e.g. Grant 1999) and may become increasingly important in a period of climate change, which may impose mismatches between breeding effort and resource availability, leading to weaker resistance to disturbances (Van Noordwijk et al. 1995; Thomas et al. 2001; Martin et al. 2008).

To date, most studies on reproduction in fluctuating environments have usually: (1) focused on predictable resources (e.g. Korpimäki and Hakkarainen 1991; Valkama et al. 2002); (2) considered conditions as stable within years and only changing among years (e.g. Korpimäki and Hakkarainen 1991; Wiebe and Bortolotti 1994; Van Noordwijk et al. 1995; Fargallo et al. 2009); (3) placed much emphasis on the impact of extreme episodes, such as droughts or floods (e.g. Bennets et al. 2002; Tryjanowski et al. 2009; Vargas et al. 2008); (4) strongly focused on breeding parameters expressed up to egg-laying (e.g. breeding density, laying date or clutch size: Seigel and Fitch 1985; Kingsford et al. 2004; Verhulst and Nilsson 2008), despite the fact that further adjustments may operate later in the breeding cycle (e.g. clutch abandonment, brood reduction: Viñuela 1999; Valkama et al. 2002); (5) examined a single reproductive parameter or few parameters (e.g. Seigel and Fitch 1985; Van Noordwijk et al. 1995; Kingsford et al. 2004). This leaves open the question of how different components may interact to fine-tune overall population-level reproduction on resources that change through time. Thus, there is a great need for comprehensive assessments incorporating the effects of dynamic changes in resource availability within and across years on multiple breeding parameters.

Wetlands associated with the floodplain of rivers and estuaries are a typical example of ever-changing and relatively unpredictable conditions, especially in arid or semi-arid climates, in which rainfall can be erratic, leading to rapid fluctuations in water regime and hydrology (e.g. Kingsford et al. 2004; Martin et al. 2008; Shine and Brown

2008). While there is agreement that changing water levels may affect the abundance, survival and reproduction of animals dependent on these ecosystems (e.g. Beissinger 1995; Béchet and Johnson 2008; Vargas et al. 2008; Tryjanowski et al. 2009), most previous studies have only examined inter-annual variations in water levels rather than within-year changes to which breeding individuals should constantly respond. Also, to the best of our knowledge, all previous studies have focused on obligate wetland species (e.g. waterbirds), whose responses may not be always representative of the suite of functional relationships existing in the whole community of organisms dependent on aquatic habitats.

In the study reported here, we analyse the long-term response of a terrestrial predator mainly dependent on aquatic prey, the black kite *Milvus migrans*, to dynamic changes in inundation levels of its main foraging habitat in Doñana National Park (SW Spain). Doñana is the largest protected wetland in Europe (>500 km<sup>2</sup>) and is located within an estuary in which vast expanses of land are left free to inundate seasonally (Díaz-Delgado et al. 2006; García and Marín 2006). Such dynamics may be typical of most river systems in more natural settings over all continents (e.g. Bren 1992; Høberg et al. 2002; Harris et al. 2005; Beja et al. 2010) but have become rare in developed countries because of intensive and widespread river regulation (e.g. Nilsson and Berggren 2000). Therefore, this system represents a unique opportunity to study the response of a wild predator to fluctuations in resource availability, which may be representative of a large suite of communities worldwide.

## Methods

### Study species

The black kite *Milvus migrans* is a medium-sized, monogamous, migratory raptor. It is an opportunistic predator that is adept at exploiting temporary situations of overabundance of relatively easy prey (Viñuela 1999, 2000), such as sudden peaks in the availability of diseased animals or vulnerable nestlings in large colonies of synchronised waterbirds.

In our population, arrival from the spring migration and settling on breeding territories usually begins in early March, the mean laying date of one to four eggs is 15 April ( $n = 1,505$  clutches) and eggs hatch asynchronously around 15 May, leading to the establishment of mass-hierarchies among the nestlings and, frequently, to brood reduction (Hiraldo et al. 1990; Viñuela 2000; Sergio et al. 2007a). Most young fledge between 15 June and 15 July. The breeding population is concentrated close to marshes,

whose proximity is over-selected for breeding and for foraging compared to local alternatives (Hiraldo et al. 1990; Sergio et al. 2005; 2009a, unpublished data from 56 radio-tagged birds). The diet is very heterogeneous and dominated by wetland birds and their nestlings, crayfish and rabbits, the latter being important only in the northern sectors of the park (see below; Hiraldo et al. 1990; Viñuela and Veiga 1992; unpublished data based on >20,000 prey remains). Therefore, kites can be considered to be the main top predators of the marsh-ecosystem and an ideal model to investigate the response of vertebrate reproduction to dynamic changes in inundation levels. Based on the above and on the results of previous studies on this and other kite populations (e.g. Sergio et al. 2003a, b, c, 2007a, 2009a), we have assumed throughout the study that wetland availability is a reliable surrogate of local resource availability.

### Study area

Doñana National Park is located within the estuary of the River Guadalquivir, along the coast of the Atlantic Ocean in south-western Spain. In a typical year, autumn–winter rainfall causes extensive flooding of vast expanses of land (Fig. 1a). The extent of such seasonal marshland (hereafter “marisma”) peaks in February–March and progressively declines thereafter with increasing spring–summer temperatures, so that little water is left by June–July (Fig. 1b; García and Marín 2006). However, this process may change radically even between successive years, spanning the whole continuum between extreme flood-years and extreme drought-years in which the marisma never floods (Fig. 1c, d).

Kites have been surveyed since 1989 in a 430-km<sup>2</sup> portion of the park, which holds a stable population of approximately 500 pairs. Apart from the marisma, the landscape is characterised by scrublands, grasslands and mobile sand dunes along the sea shore. Mature trees suitable for nesting are mostly present as scattered cork oaks *Quercus suber* or as large plantations of *Eucalyptus* trees or of stone pines *Pinus pinea*. Overall, heterogeneity can be very pronounced, mostly because of variation in agro-forestry management among different properties before the institution of the park. For example, tree density may change radically between large blocks of dense *Eucalyptus* plantations and large expanses of open dehesas (grassland with scattered oaks). Therefore, we divided the study site in sub-areas (hereafter “Units”; Fig. 2) based on such abrupt changes in landscape composition. Applying this method, all Units held at least ten breeding pairs in each year of the study (range 20–121 pairs for shoreline Units, 10–31 pairs for more inland Units). The results of an alternative, complementary analysis which focused exclusively on the 14 shoreline Units were similar and are presented in Appendix 2 in the Electronic Supplementary Material (ESM).

### Field procedures

Kites were censused in the pre-incubation period by observing territorial displays, nest material transfers and the presence of birds perched in or near a nest on multiple days. Pairs were classified as laying or non-laying only when their nests could be checked weekly during the incubation period. This ensured that we did not classify as non-laying females those that actually laid eggs but lost their clutch soon afterwards. Whenever possible, nest contents were checked three times: first, during incubation to assess clutch size; second, just after hatching to estimate hatching success and brood size; third, when the nestlings were 40–45 days old to record the number of reared young and ring them (Sergio et al. 2005; Blas et al. 2009; nestlings fledge at 48–50 days old). Laying date was calculated through a regression of age on the length of the eight primary of the first-hatched nestling of the brood (Viñuela and Bustamante 1992). Because feather growth is linear up to fledging (Viñuela and Bustamante 1992), this parameter is considered the best morphometric measure to backdate the birth date of each chick. Overall, data were available for 4,628 nesting attempts.

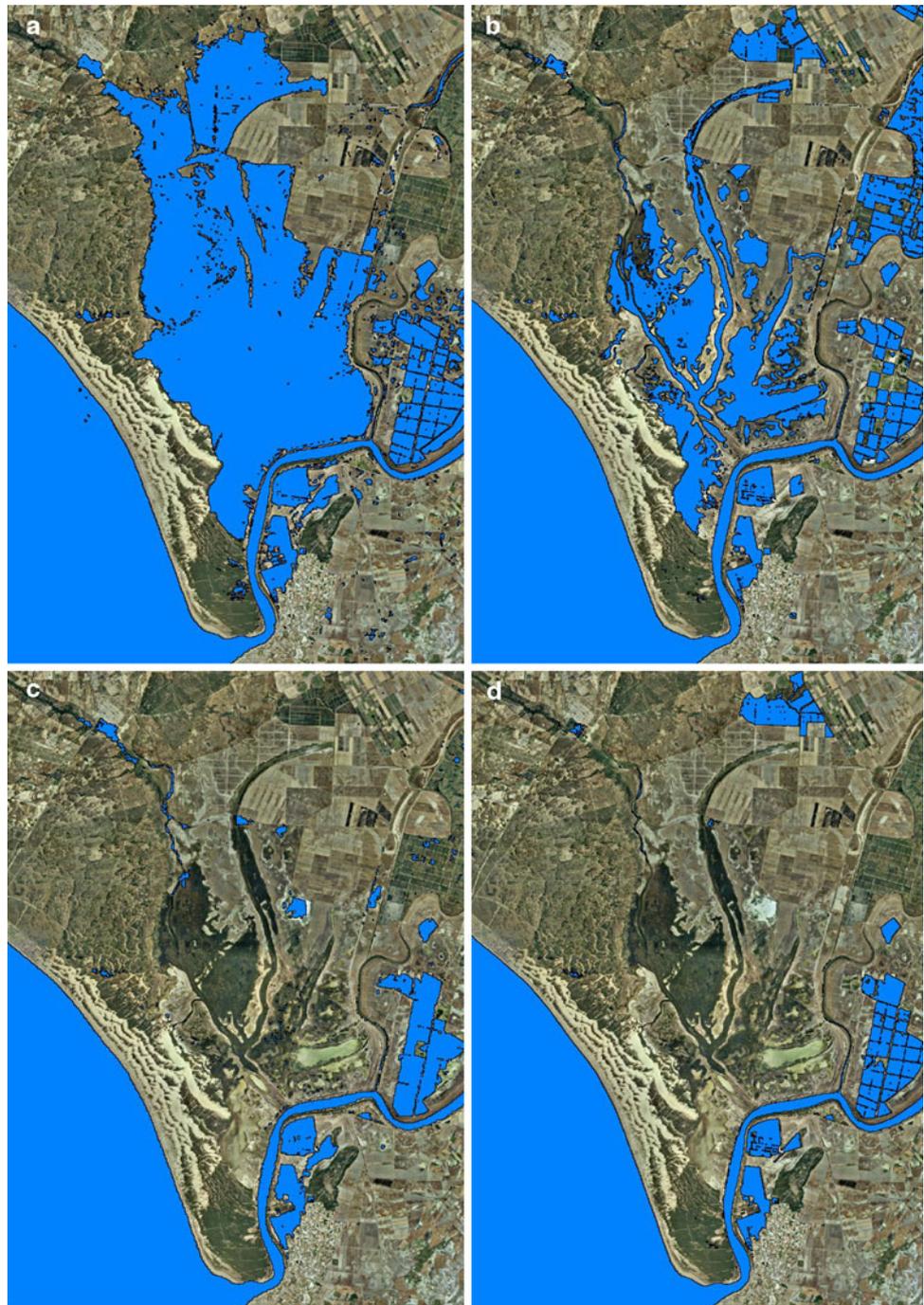
### Estimation of inundation levels and rates

Inundation levels were calculated by accessing all the available cloud-free Landsat MSS, TM and ETM+ scenes for the Doñana region during the period 1975–2008 (>300 images). Images were radiometrically corrected, transformed into reflectance values and normalised to a reference image to produce final inundation masks based on pixels of 30 × 30 m (details in Díaz-Delgado et al. 2006; Bustamante et al. 2009; examples in Fig. 1).

Because we were interested in testing the effect of inundation levels at key dates comparable among years (see third paragraph of “Hypothesis and statistical testing” and Appendix 1 in the ESM) and because Landsat images were not always available on such exact dates (e.g. because of cloud cover), we linearly interpolated the values of the images available before and after each target key date. This method was substituted by the use of the values predicted by a quadratic or cubic regression of “m<sup>2</sup> of land estimated as inundated in each sample” on the date when such regressions explained >95% of the variance in the dependent variable.

To characterise the inundation levels of each Unit of Fig. 2, we estimated water levels in a polygon built by: (1) drawing 2-km circular buffers around all the nests used at least once in that Unit during 1989–2008, and (2) merging the buffers in a single polygon, hereafter called “buffer-polygon”. Because >90% of the foraging locations of our kites equipped with GPS radio-tags were within 2 km of

**Fig. 1** Examples of inundation of the marisma of Doñana National Park (Spain) at progressive dates during the breeding cycle of the black kite *Milvus migrans* and in different years. **a, b** Representative inundation masks based on Landsat images of 3 March and 26 June 1996, a year of high flooding, **c, d** representative inundation masks of conditions on 27 March and 15 June 1993, a drought year. Units that look like an artificial grid of plots in the east and north-east portion of the images are rice plots that are artificially inundated, sometimes late in the season. These areas are scarcely used by breeding kites, and their surface was never included in calculations of inundation-levels (based on data from breeding individuals equipped with GPS/satellite tags)



their nest (unpublished data), such sample-plots are expected to reflect the inundation levels of the main foraging grounds of the population of each Unit.

#### Hypotheses and statistical testing

We used time-series analysis to explore the long-term trend of inundation levels of the marisma during the kite breeding season (March–July) over the last 22 years (1987–2008) for which adequate Landsat images were available. Periodo-

grams, autocorrelation and partial autocorrelation function plots (ACF and partial ACF) were used to check for temporal autocorrelation and cyclic patterns (Crawley 2007). To test the seasonal, within-year predictability of future inundation levels based on current ones, we correlated water levels for each of the Units at the beginning of the breeding season (15 March) with the levels observed on 15 June, which is during the main fledging period of peak food demand for kites. We used a binomial test to examine the preponderance of correlations in which >50% of the



**Fig. 2** Sampling units in which the overall study area was sub-divided (see “Methods”). Units 1–14 were located along the shoreline of the marshes and Units 15–21 were more inland

variability in water levels in June could be explained by water levels in March. We assumed that the incapability to predict more than 50% of the future variations in water levels would imply a marked level of uncertainty in future resource levels (e.g. Beissinger 1986; Shine and Brown 2008).

We hypothesised that kites could respond to resource availability by altering through active or passive mechanisms (see below) multiple components of breeding performance during progressive key periods of the reproductive cycle (see below and Appendix 1 of the ESM). In particular, we hypothesised that resource levels could constrain or cause adjustments in: (1) the decision of whether to settle or not on a territory, with repercussions on population density; (2) the likelihood of laying eggs or skipping reproduction; (3) the advancement or delay of egg laying; (4) the number of eggs laid; (5) the rate of hatching success; (6) the frequency of brood reduction; (7) the number of nestlings raised to fledging age. This decomposition of the reproductive cycle into relevant parameters and progressive episodes allowed us to test whether, how and when population-level reproduction was adjusted to available resources. In this respect, two clarifications are important. (1) Firstly, the sample unit in all our analyses is a group of nests, i.e. a population. Even though breeding adjustments to resources will operate at the individual level, here we are interested in what the majority of individuals are doing,

which leads to the emergent, average pattern of population response to resource fluctuations. In the “Discussion” we elaborate on previous results on individual-level mechanisms which are consistent and conducive to the population patterns reported below. (2) Secondly, breeding adjustments to resources could be driven by: (a) active tactics, such as the decision of how many eggs to lay, and (b) more passive mechanisms, such as brood reduction, which may be the result of an unpredictable constraint (e.g. food shortage). However, drawing the boundary between these two extremes is often difficult (Wiebe and Bortolotti 1994); for example, brood reduction is usually considered to be mediated by asynchronous hatching, which may be actively imposed by the parents (e.g. Viñuela 1999, 2000; Valkama et al. 2002). Thus, under a scenario of future unpredictability, parents could promote the possibility of brood reduction via asynchronous hatching as a potential optional adjustment to suddenly deteriorating conditions (i.e. an active tactic which leads to resource adjustments through chick mortality). Because such active and indirect mechanisms may simply be two extremes of a continuum and drawing the line between them may be difficult, hereafter we refer to these collectively as “breeding adjustments”.

To test the relationship between inundation levels and the above breeding parameters, we (1) decided upon key dates in the reproductive season when each breeding component could be affected by resource levels (e.g. the mean laying date in this population is 15 April, so 15 April was taken as the relevant date to characterise parameters such as the decision to lay eggs and clutch size; see dates in Appendix 1 in the ESM), (2) assessed inundation levels for each of the above dates in buffer-polygons and (3) related each component of breeding performance to inundation levels by means of generalised linear mixed models (GLMMs with normal errors and an identity link function; R Development Core Team 2009).

Because Units were repeatedly sampled (pseudoreplicated) through the years, all GLMMs were built by fitting year and Unit-identity as random terms (Crawley 2007). The rationale for adding further explanatory variables is based upon the following explanations.

1. If resources were temporally auto-correlated, kites could predict their levels in the future. In such a scenario, resource levels in the early stages of the breeding cycle could predict breeding parameters expressed later in the season (e.g. resources in pre-incubation could predict success rates at fledging). On the contrary, if resource levels are unpredictable, breeding parameters should be solely related to current resource levels. Consequently, to discriminate between such possibilities, the models were always fitted with the inundation levels for the target date and for all the other potential previous dates.

2. Kites could use the rate of drying/flooding of the marisma as a predictive cue for breeding decisions, rather than its current absolute inundation level. Alternatively, they could use both cues in conjunction. For example, they could decide to lay larger clutches in areas with high and slowly declining water levels rather than in areas of low and rapidly declining resources. For this reason, we calculated the mean daily rate of change in water levels during the pre-laying, incubation, nestling and fledging period. Such daily rates and their interactions with absolute water levels were fitted as additional explanatory variables.
3. Units in the northern sectors of the park (Units 10–14 and 20–21 in Fig. 2) held high densities of rabbits, a locally predominant prey in the diet, whose consumption is associated with high kite density and productivity (Viñuela and Veiga 1992; Viñuela et al. 1994). Rabbits were most abundant close to the marisma but also occurred in isolated, high-density patches more inland (Palomares 2001), which may distemper the dependence of kites on wetlands in such Units. On the contrary, rabbits were virtually absent from the southern sectors of the park. For example, during standardised road-counts conducted in June between 2007 and 2009, rabbit abundance was estimated on average to be 26.2 individuals/km in the northern sectors but only 0.28 individuals/km in the southern sectors, a 93-fold difference in occurrence. To reflect such an abrupt variation in the availability of a key prey that may condition the dependence of kites on inundation levels, we classified each Unit as holding high (northern Units, value = 2) or virtually zero (southern Units, 1) rabbit abundance. This dummy variable and its interaction with inundation levels were added as explanatory variables to all models. Even if more detailed, quantitative estimates of rabbit abundance would have been more desirable, unfortunately these were not available on a per-Unit basis for the 22 years of study.
4. In models predicting breeding density, we added the density of mature trees potentially suitable for breeding in each Unit as a covariate to control for among-Units differences in nest-substrate availability. Suitable trees were individually mapped in ground surveys conducted by researchers with >5 years experience in surveying kites (Sergio et al. 2005;  $n = 29,683$  mapped trees).
5. In models on breeding success, the breeding density in each Unit/year was added as a covariate to control for density-dependence.
6. To control for the potential effect of unmeasured environmental factors which could change between inland and shoreline Units, we fitted to all models a dummy variable “Inland”, which classified each Unit as “shore-

line” (dummy value = 1; Units 1–14 in Fig. 2) or “inland” (value = 2; Units 15–21 in Fig. 2).

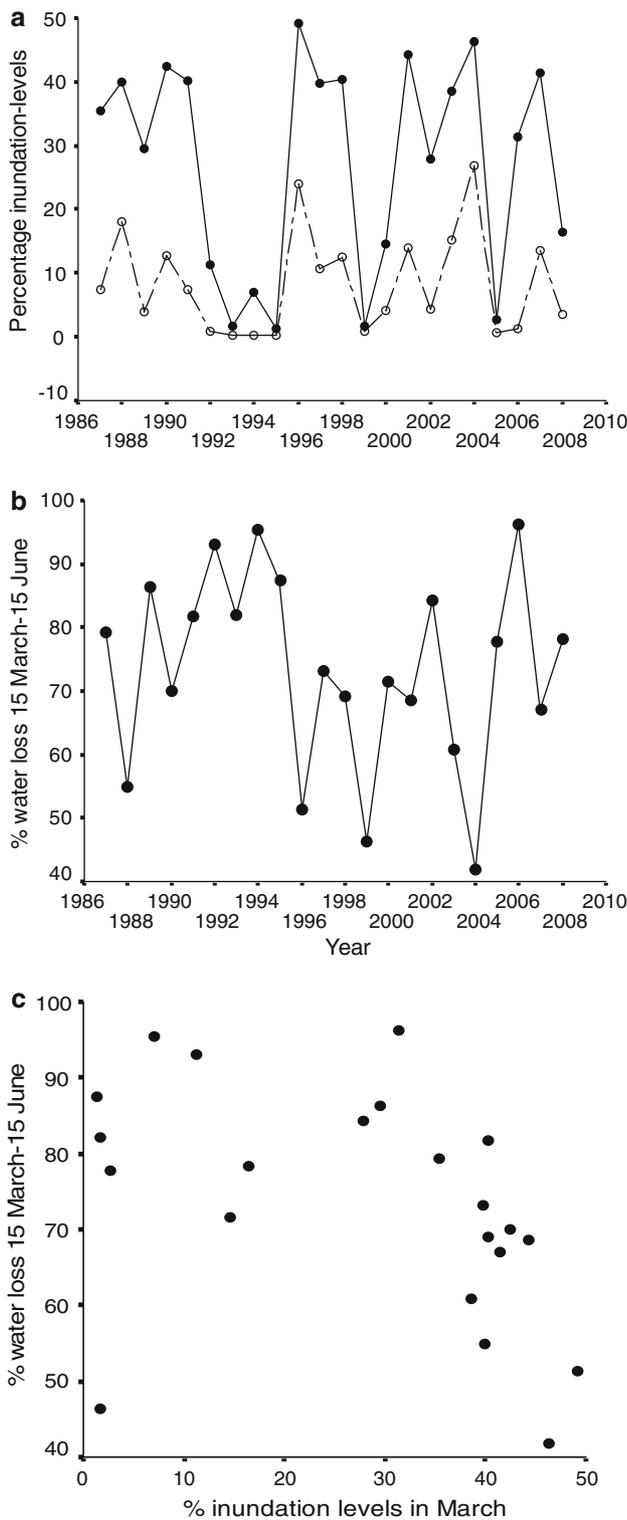
Finally, to gain an understanding of the breeding parameters that most contributed to final reproductive output, we regressed for each Unit the mean number of fledged young on the other components of breeding performance outlined above (laying date, clutch size, brood reduction, etc.) by means of a multiple regression.

In all analyses, the sample-unit is the mean value of a reproductive component (e.g. clutch size) for a Unit in a given year. To be included in the analyses, each mean had to be based on at least 15 checked nests for shoreline Units (range 15–121) or ten checked nests for inland Units (10–31; based on plateau accumulation curves and constraints of low sample sizes in inland Units). Models were built through a backward stepwise procedure as follows: (1) all explanatory variables were fitted to a (maximal) model, extracted one at a time from this maximal model and the associated change in model deviance assessed by a likelihood ratio test (Crawley 1993); (2) in parallel, the least significant variables were sequentially removed by a likelihood ratio test from the maximal model until a minimal adequate model was obtained that only retained significant effects (Crawley 2007); (3) at each step of the two above procedures, we calculated the small sample-corrected Akaike's information criterion (AICc) of each model and considered the final competitive model to be the one with the lowest AICc (Burnham and Anderson 2002). In all analyses, the three methods of model selection were in agreement on the most competitive model. To minimise over-parameterisation, we ensured that never more than  $n/3$  variables were fitted to each maximal model (Crawley 2007). When a minimum adequate model was found, we further tested whether curvilinear effects (quadratic or cubic) of the inundation variables that entered the model would provide a better fit (lower AICc) than linear effects. All statistics were implemented in R.2.9.2 (R Development Core Team 2009), all tests are two-tailed, statistical significance was set at  $\alpha < 0.05$  and all means are given  $\pm 1$  standard error (SE).

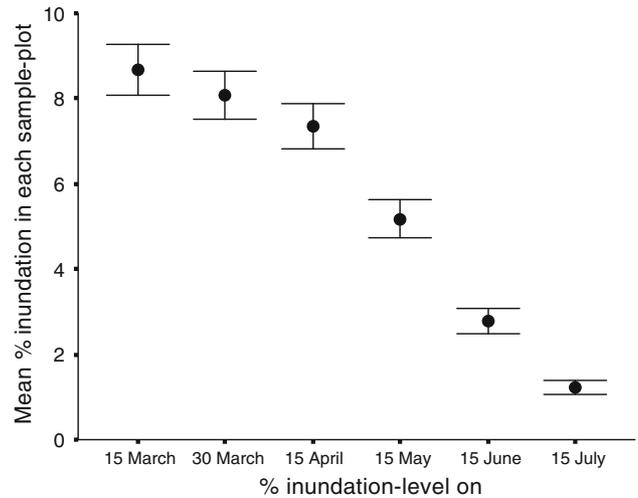
## Results

### Inundation levels and their predictability

In Fig. 3a we show the estimated inundation levels for 15 March and 15 June since 1987 in the marisma as a whole. Periodograms, ACF-plots and partial ACF-plots gave no indication of cyclicity or temporal autocorrelation among years for any of the six sample dates (15 March, 30 March, 15 April, 15 May, 15 June, 15 July). For each of these



**Fig. 3** **a** The 22-year time-series of inundation levels measured on 15 March (filled circles) and 15 June (open circles) which are at the beginning and the end of the breeding season of black kites, respectively. **b** Percentage water loss between 15 March and 15 June each year. Water loss was calculated as: [(water levels on 15 March) – (water levels on 15 June)]/(water levels on 15 March). **c** Percentage water loss between 15 March and 15 June in relation to initial water levels on 15 March



**Fig. 4** Mean progressive decline in inundation levels along the kites breeding season in 21 sample Units in the 22-year time-series (1987–2008)

dates, there was no trend in inundation levels along the 22 years of the time-series (all  $t < 0.97$ ,  $P > 0.34$ ).

Within years, inundation levels declined steadily within all 21 Units along the kites’ breeding season (Fig. 4). However, the percentage decline in water levels between 15 March and 15 June varied enormously across years (Fig. 3b) and was poorly related to initial flooding levels (see noisy scatter in Fig. 3c). When water levels observed on 15 June were regressed on those observed on 15 March in each of the 21 Units across years, there was no preponderance of predictable relationships, with  $R^2 \geq 0.50$  (binomial test,  $P = 0.12$ ). The relationships were even weaker when inundation rates were used rather than absolute water levels (binomial test,  $P = 0.41$ ). Using higher cutoff-point values of  $R^2$  (e.g. 0.60, 0.70) resulted in a preponderance of relationships below the  $R^2$  cutoff point, implying even lower predictability (binomial test, all  $P \leq 0.003$ ). Based on these results, we considered inundation levels to be mostly unpredictable in the future both within and across years.

**Inundation levels and reproduction**

Breeding density increased with rabbit abundance, with the availability of potential nesting trees and with the inundation rate for 15–30 March (Table 1, model a); lower densities were associated with higher rates of water loss in this early settling-period.

No variable significantly predicted the percentage of breeding pairs in each Unit (all candidate models within 0.8 AICc-units of the null model, all  $t \leq 1.57$ , all  $P \geq 0.12$ ). Laying date was more advanced in shoreline than inland Units and became earlier with higher inundation levels on 15 and 30 March and with lower levels of water-loss in the

**Table 1** GLMM models testing the relationship between breeding rates and inundation levels in a black kite (*Milvus migrans*) population

Effect on (sample size)	Variable <sup>a</sup>	21 shoreline + inland Units			
		Parameter estimate ± SE	<i>t</i>	<i>P</i>	AICc
Model a: Density ( <i>n</i> = 135)	Tree density	0.48 ± 0.15	3.16	0.002**	259.0
	Rabbit <sup>b</sup>	0.25 ± 0.14	1.78	0.076 <sup>+</sup>	
	Rate 15–30 March	6.31 ± 3.19	1.98	0.050*	
	Units-ID <sup>c</sup>		126.86	<0.001***	
Model b: Laying date ( <i>n</i> = 61)	(15 March) <sup>2</sup>	−0.21 ± 0.09	−2.50	0.016*	−219.7
	(30 March) <sup>2</sup>	−0.31 ± 0.12	−2.61	0.012*	
	Rate 30 March–15 April	−0.63 ± 0.35	−1.81	0.077 <sup>+</sup>	
	Inland <sup>d</sup>	0.05 ± 0.02	2.71	0.009**	
	Year <sup>c</sup>		13.87	<0.001***	
Model c: Clutch size ( <i>n</i> = 58)	Density	−0.13 ± 0.06	−2.33	0.025*	−33.2
	Rabbit	0.21 ± 0.07	3.08	0.004**	
	Year		8.98	0.003**	
Model d: Hatching success ( <i>n</i> = 57)	(15 May) <sup>2</sup>	0.96 ± 0.28	3.44	0.001**	−40.8
	Rabbit	0.18 ± 0.06	3.06	0.004**	
	Breeding density <sup>c</sup>	−0.09 ± 0.05	−1.83	0.075 <sup>+</sup>	
Model e: Brood reduction ( <i>n</i> = 48)	15 June	−1.21 ± 0.33	−3.70	0.001**	−14.9
Model f: No fledged young ( <i>n</i> = 112)	15 June	1.43 ± 0.42	3.44	<0.001***	
	Rabbit	0.24 ± 0.06	4.16	<0.001***	
	Rabbit 15 June	−1.04 ± 0.38	−2.77	0.007**	
	Inland <sup>d</sup>	−0.17 ± 0.05	−3.58	<0.001***	

AICc, Small sample-corrected Akaike's information criterion

<sup>+</sup>  $P < 0.1$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

<sup>2</sup> Quadratic effect

<sup>a</sup> Explanatory variables with a date-name represent the inundation levels observed on that date (e.g. 15 March represents the measurement of the inundation level observed on 15 March in each sample-polygon). Rate-variables represent the mean daily rate of water-loss for the period specified in each variable name (e.g. Rate 15–30 March represents the rate of water-loss for the period 15–30 March)

<sup>b</sup> Dichotomous variable: 1 = units with very scarce rabbit availability (Units 1–9 and 15–19 in Fig. 2); 2 = Units with high rabbit availability (Units 10–14 and 20–21)

<sup>c</sup> Random effect. Significance tested by means of an analysis of variance (ANOVA) when extracting the random-effect from the model (Crawley 2007)

<sup>d</sup> Dichotomous variable: 1 = shoreline Units close to the marshes (Units 1–14 in Fig. 2); 2 = inland Units (Units 25–21)

<sup>e</sup> Residuals of a regression of density (Number of pairs/10 km<sup>2</sup>) on the surface of each Unit

period 30 March–15 April (Table 1, model b; Fig. 5a). Clutch size increased with rabbit abundance and was negatively density dependent (Table 1, model c).

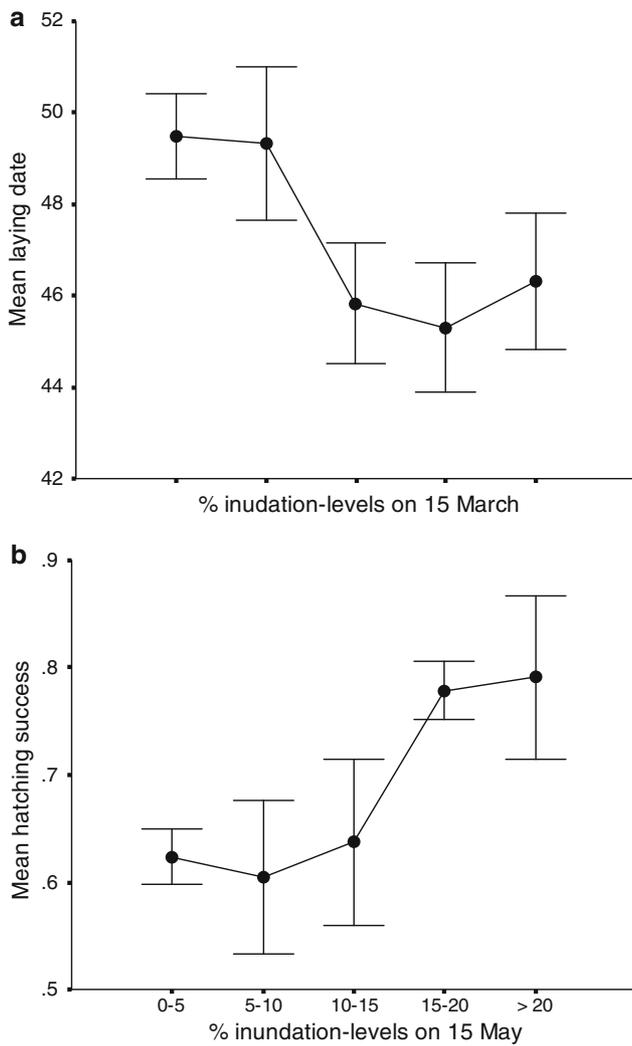
Hatching success increased with rabbit abundance and with inundation levels on 15 May and was negatively density dependent (Table 1, model d; Fig. 5b). The incidence of brood reduction declined with inundation levels on 15 June (Table 1, model e; Fig. 6a).

The mean number of young raised to fledging in each Unit was higher in shoreline than inland Units and increased with rabbit abundance and with inundation levels in June (Table 1, model f; Fig. 6b). An interaction was also significant: the relationship between the number of fledged young and inundation levels was steeper in Units with low rabbit abundance (Fig. 6b).

In decreasing order of importance, the reproductive components that contributed most to the final breeding output (mean number of fledged young) in each Unit, as determined in a stepwise multiple regression, were brood reduction ( $\beta = -0.53$ ,  $t = -5.86$ ,  $P < 0.001$ ), hatching success ( $\beta = 0.36$ ,  $t = 3.83$ ,  $P < 0.001$ ), percentage of pairs laying eggs ( $\beta = 0.30$ ,  $t = 3.36$ ,  $P = 0.002$ ) and laying date ( $\beta = -0.24$ ,  $t = -2.50$ ,  $P = 0.018$ ;  $R^2$  of overall model = 0.78, AICc = −67.8). The contributions of density and clutch size were never significant (all  $t \leq 1.28$ ,  $P \geq 0.22$ , AICc  $\geq -61.8$ ).

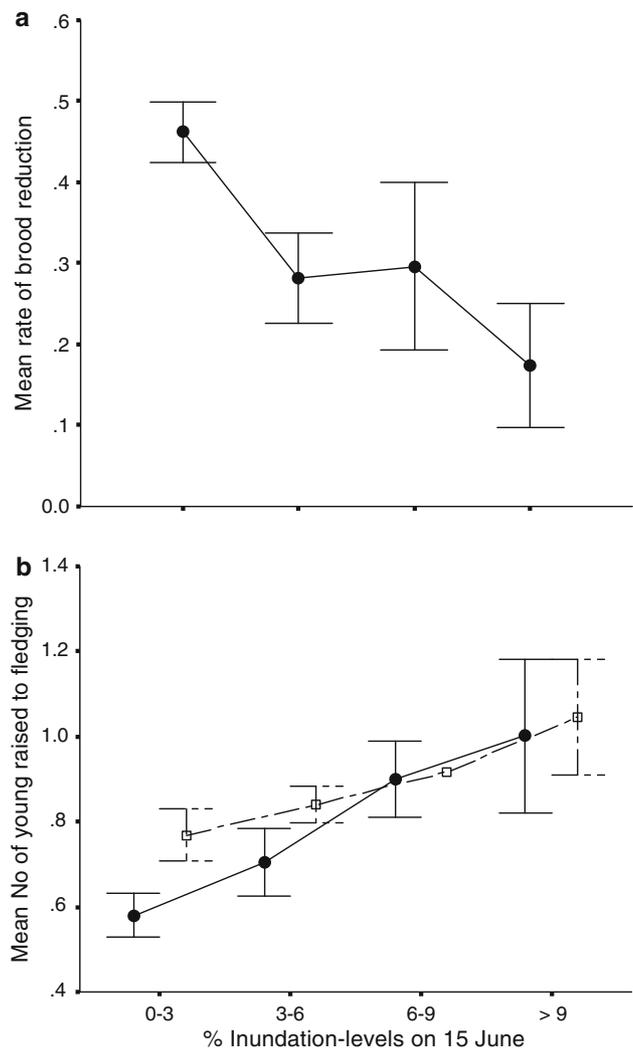
## Discussion

Multiple lines of evidence obtained from our study suggest that kites depended on an unpredictable resource base.



**Fig. 5** **a** Relationship between mean laying date ( $n = 61$ ) and inundation levels on 15 April (the mean laying date of the population). **b** Relationship between mean hatching success ( $n = 57$ ) and inundation levels on 15 May (the mean hatching date of the population)

Firstly, inundation levels fluctuated widely among years, with no clear trend or cyclicity, so that years of high flooding could be followed by years of extreme drought (Fig. 3). Secondly, even if water levels always declined through the breeding season (Fig. 4), their rate of water loss changed radically among years (Fig. 3b, c), and kites would have been rarely able to predict more than 50% of the variation in future water levels. This implies that similar conditions between years at the beginning of breeding could evolve into different conditions by the end of breeding (e.g. compare years 2005 and 2006, or 2001 and 2004 in Fig. 3a). Finally, rates of predictability and water loss were similar to those reported in other systems considered as unpredictable. For example, the autocorrelation in inundation levels between the beginning and the end of a 4-month breeding season was 0.39 in our study and 0.38 in the Florida Ever-



**Fig. 6** Effect of inundation levels in June on: **a** the incidence of brood reduction ( $n = 48$ ); **b** the mean number of young produced by the population ( $n = 112$ ) under conditions of high (open squares) or low (filled circles) availability of rabbits (one of the main prey items in the diet, see text)

glades (Beissinger 1986), a wetland ecosystem also classified as unpredictable (Beissinger 1986). Therefore, dynamical changes in resources within years were superimposed on marked fluctuations among years. Such boom and bust dynamics, with rapid oscillations between good and bad years, may be typical of wetland systems, which are usually characterised by a perpetual non-equilibrium status, especially in arid or semi-arid climates (e.g. Beissinger 1995; Kingsford et al. 2004; Winne et al. 2006).

Populations and breeding rates are usually thought to be limited by the resource which is shortest in supply (e.g. Clutton-Brock 1988; Newton 1998). Therefore, when resource levels will be limiting sometime in the future in an unpredictable manner, allocating breeding effort may become difficult and mistakes can be costly

(Thomas et al. 2001). Under such scenario, there are various non-exclusive adjustments that can lower such costs. Below, we consider those that could apply to our population.

- (1) Under a regime of unpredictability, components of breeding expressed early in the reproductive cycle cannot be planned on the basis of current resources because these may not be predictive of final, future levels. Given such uncertainty, early breeding components could be better tuned on more predictable secondary factors, while waiting for main resources to become easier to assess (a waiting, conservative strategy). Our study provided partial support for this concept: (1) the effect of inundation levels on breeding became more pervasive for the components expressed at later stages of the breeding cycle; (2) early components were mostly related to more predictable social and environmental factors, such as breeding density, the presence of rabbit-prey nearby or the availability of suitable trees (Table 1). The relationship between breeding density and tree abundance, coupled with previous analyses, further suggests that the population was saturated at a relatively stable, high density (see further support in Sergio et al. 2005, 2007, 2009b). An invariant, crowded population could be integral to a waiting strategy of “relaxed” territoriality where individuals initially settle in high numbers only to adjust their effort later.
- (2) Theoretical models suggest that, in unpredictable environments and in species in which adult survival is high relative to that of dependent young, clutch size (i.e. the initial allocation of resources to reproduction, which puts a ceiling on maximum offspring production) should be conservatively small and not related to current resource levels (Goodman 1979; Stearns 1999). In agreement with this, clutch size in our population was unrelated to inundation levels and was small for a bird of this size ( $2.10 \pm 0.02$ , mode = 2, range 1–4,  $n = 1,492$  clutches; see Newton 1979 for comparative data on other raptors of similar size). Interestingly, the exact same pattern of small clutches ( $2.66 \pm 0.03$ , mode = 3, range 1–4) unrelated to water levels has also been highlighted as an adaptation to unpredictable resources in the snail kite *Rostrhamus sociabilis*, a smaller raptor also dependent on unpredictable hydrological regimes (Beissinger 1986; 1995; Snyder et al. 1989).
- (3) If resources will be unpredictably limiting in the future, advantages would be conveyed by adjustments facilitating the tracking of resources in real time at the moment when these become limiting (e.g. later on in the season via chick mortality facilitated by asynchronous hatching). This concept is supported by various

results. Firstly, final breeding output was mainly determined by components of reproductive performance expressed late in the breeding cycle, such as hatching success and brood reduction. Secondly, such later components were those most affected by inundation levels and were always best related to the inundation levels observed simultaneously to the period in which they were expressed. For example, hatching success was related to the water levels of 15 May, when most pairs will be hatching eggs, and not to water levels in March or April. Thirdly, in this population, hatching success and brood reduction would be the main mechanisms allowing late adjustments of breeding rates to resource levels when these start to be limiting. Both components were well related to inundation levels. In particular, earlier work on this population at the individual level showed that brood reduction peaks when nestlings are approximately 20 days old, that it may occur up until they are approximately 30 days old and that it is related to the establishment of mass hierarchies in the brood. Mass hierarchies are dependent on the asynchronous commencement of incubation and on the rate of growth of the first-born nestling in this early period of life which, in turn, is related to parental food provisioning (Viñuela 1999, 2000). Consistent with this, inundation levels in mid-June probably captured well the trophic conditions experienced by kites during the first month of life of the nestlings. Poor conditions in this key period would then lead to generalised low parental provisioning, slow growth of senior chicks and high nestling mortality through siblicide and starvation, providing an interesting link between environmental constraints, individual life-history tactics (decisions on asynchronous commencement of incubation) and emergent population-level properties. Under this scenario, a relatively small, invariant and asynchronous clutch could be integral to an overall bet-hedging strategy in which clutch abandonment and chick mortality are the main mechanisms that eventually fine-tune breeding rates on unpredictable resource levels. We stress that such mechanisms may incorporate both: (1) environmental constraints (e.g. food shortage) which cannot be counteracted by parental tactics, and (2) parental life-history tactics (e.g. asynchronous laying) which may indirectly facilitate such tuning mechanisms when conditions get unpredictably worse (e.g. Wiebe and Bortolotti 1994). More detailed, individual-level analyses on marked individuals will be needed to further investigate such possibilities.

- (4) Finally, the effect of unpredictable disturbances may be buffered by the availability of refugia. For example, species with high mobility, such as waterbirds, may resist

droughts by escaping to less-affected wetlands (e.g. Bennets et al. 2002; Vargas et al. 2008; Béchet et al. 2009). In our system, droughts occurred too late in the season and were generalised over too vast areas to allow dispersal. However, the availability of a terrestrial prey species, the rabbit, alleviated the dependence of part of the population on the inundation disturbance. In this sense, such a portion of the population could act as a source during drought years. Dietary opportunism may have thus facilitated resistance to disturbance without a need for dispersal, providing some sort of “behavioural refugia”, similar to the aestivation strategies of some species with low mobility (Winne et al. 2006).

In conclusion, kites likely respond to an unpredictable environment through multiple complementary adjustments. As the season progressed and local predictive information became more available (Wingfield 2008), a waiting strategy based on a conservatively small, invariant and asynchronous clutch gave way to real-time tracking mechanisms mediated by progressive adjustments to current resource levels, so that population-level breeding rates were determined and fine-tuned on resources rather late in the season, an unusual pattern in raptor populations (Newton 1979). Behavioural flexibility, such as dietary opportunism, probably promoted further resistance to resource oscillations. Such adjustments are in marked contrast to those reported for the only other raptor on which similar analyses have been conducted, the snail kite. In this species, reported adaptations to cope with unpredictable water levels include multiple brooding per year, frequent mate desertion and high rates of dispersal to new breeding grounds (e.g. Beissinger 1986, 1995; Bennets et al. 2002; Martin et al. 2008), none of which have been observed in our population. All of this suggests a complex suite of adjustments and life-history tactics employed by different, even closely related species, to cope with the complex task of predicting the future in an unpredictable environment. Given that all ecosystems will show some degree of long-term predictability on which is superimposed some degree of unpredictability (Shine and Brown 2008), tracking adjustments, such as the ones we depicted here, are likely to be commonplace in most communities.

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