

Ecological factors influencing the breeding distribution and success of a nomadic, specialist predator

J. Terraube · B. E. Arroyo · A. Bragin · E. Bragin · F. Mougeot

Received: 6 June 2011 / Accepted: 23 March 2012
© Springer Science+Business Media B.V. 2012

Abstract Ecological specialization can explain the declining status of many species in the face of current global changes. Amongst specialists, nomadic predators present conservation biologists with many challenges, mainly because of the difficulty of studying highly mobile individuals over time and across very large areas. For these species, the relative influence of prey abundance, habitat heterogeneity and arrival time at the breeding grounds on breeding parameters remains poorly understood. We studied the factors influencing variation in breeding numbers and performance of a declining nomadic specialist raptor, the Pallid Harrier *Circus macrourus*, in north-central Kazakhstan. During a 5-year period, we recorded large inter-annual variation in vole abundance in the main study area, and differences between habitats. We also recorded a strong numerical response of breeding Pallid Harriers to inter-annual changes in local vole abundance. From a 13-year dataset on breeding harriers in the same area, harrier numbers appeared to vary cyclically, with an interval between peaks of approximately 6 years. At a broader, regional scale, variations in Pallid Harrier abundance appeared asynchronous, suggesting a regional

J. Terraube
Natural Research Ltd, Banchory Business Centre, Burn O'Bennie Road, Banchory AB31 5ZU, UK

J. Terraube · B. E. Arroyo
Instituto de Investigación en Recursos Cinegéticos, IREC-CSIC-UCLM-JCCM, Ronda de Toledo s/n,
13005 Ciudad Real, Spain

J. Terraube (✉)
UMR Biodiversité Gènes et Communautés, INRA, 69, Route d'Arcachon, 33610 Cestas, Spain
e-mail: jtterraube@gmail.com

A. Bragin
Moscow Pedagogical State University, Kibalchicha Street 6, Moscow, Russia 129278

E. Bragin
Science Department, Naurzum National Nature Reserve, Kustanay Oblast, Naurzumski Raijon,
Karamendi 459730, Kazakhstan

F. Mougeot
Estación Experimental de Zonas Áridas (EEZA-CSIC), Ctra. de Sacramento s/n La Cañada de San
Urbano, 04120 Almería, Spain

redistribution of harriers between years. Reproductive success depended on local vole abundance, but also on timing of breeding and nesting habitat. Clutch size, nest success and fledged brood size increased with vole abundance. Late breeders had smaller clutches and apparently lower hatching rates than early ones, possibly as a result of the interplay between their probable poorer body condition and habitat-specific variation in predation rates. In true nomadic specialist predators, such as Pallid Harriers, breeding success may therefore depend on a complex interplay between spatial variation in prey abundance, habitat composition and timing of breeding attempts. One of the factors influencing the start of breeding is the length of time taken to prospect between different breeding sites, which in turn may depend on the predictability of spatial and temporal variation in vole abundance. These results have important conservation implications, as changes in climate and habitat could affect spatial and temporal variations in vole abundance, with possible consequences for timing of breeding, food availability and, ultimately, the reproductive success of this declining nomadic predator.

Keywords Nomadic predator · Breeding parameters · Prey abundance · Habitat composition · Global changes · Conservation · Kazakhstan · *Circus macrourus*

Introduction

Specialist species are often more threatened than generalists, possibly because specialisation makes them less able to move or adapt in response to environmental change (Clavel 2007). Indeed, sensitivity of birds to habitat loss and fragmentation has been linked to habitat and dietary specialization (Owens and Bennett 2000; Shultz et al. 2005). Among birds, some predators specialize on prey that fluctuates in abundance asynchronously over large areas. Such predators are typically nomadic, moving between breeding areas according to where their preferred prey is more abundant and spending a considerable amount of time prospecting to find such areas (Korpimäki and Norrdhal 1991; Tannerfeldt and Angerbjörn 1996; Terraube 2010). Studying nomadic species remains a real challenge for ecologists and conservation biologists because of their high mobility and the necessity to gather information at more than one spatial scale. As a result, studies on the population ecology of nomadic species remain scarce.

Understanding the factors determining variation in breeding numbers and performance is crucial to the effective management and conservation of many species. Despite being highly mobile, nomadic specialist predators are particularly sensitive to changes in the dynamics of their prey, as predator demographic parameters are tightly linked to variation in prey density (Tannerfeldt and Angerbjörn 1996). Currently, weakening population cycles of rodents are being increasingly reported in sub-arctic and boreal areas, where many predators of these rodents are in decline (Hörnfeldt et al. 2005, but see Brommer et al. 2010, for a case of population cycle coming back after disappearance). Nevertheless, in nomadic species, the relative effects on breeding parameters of habitat heterogeneity, food abundance and arrival time at the breeding grounds are poorly understood. Consequently, understanding the factors determining spatial and temporal variation in breeder numbers and reproductive success is crucial to assessing the risks posed to specialists by global environmental change, and developing targeted conservation programmes for these species (McKinney and Lockwood 1999; Warren et al. 2001; Julliard et al. 2004).

Breeding habitat quality can influence reproductive and survival rates through variations in predation risk (Caro 2005), microclimatic conditions at the breeding site (Walsberg

1985) or food supply in nearby foraging habitats (Klopfer and Ganzhorn 1985; Hakkarainen et al. 1997; Newton 2003). The dynamics of specialist nomadic predator populations are strongly affected by inter-annual changes in the availability and distribution of prey (Angerbjörn et al. 1999; Nielsen 1999), giving rise to variation in local breeding densities, primarily through immigration and emigration of breeding individuals in response to feeding conditions (Newton 2007). Furthermore, some nomadic specialist raptors are long-distance migrants, for which decisions made prior to and during migration from the wintering to the breeding grounds can have major effects on reproductive success and survival (Møller 1994; Berthold 2001). Such effects may be mediated by factors such as condition upon arrival on the breeding grounds, or arrival date. In addition to their having to find areas of high prey abundance at the start of the breeding season, nomadic migrants are therefore also subject to additional costs and constraints associated with long migration.

The Pallid Harrier *Circus macrourus* is a specialist predator of voles (Terraube et al. 2011) and a long-distance migrant (birds breed in Russia and Central Asia, and winter in India or Africa; Ferguson-Lees and Christie 2001; Terraube et al. 2012). To date, little is known about the relationship between voles and harrier breeding parameters (although see Terraube et al. 2011 for preliminary data). Nomadic behaviour in the Pallid Harrier has been described through large changes in numbers between years at a local scale (Bragin 2003), and more recently through satellite tracking (Terraube 2010; Terraube et al. 2012). Substantial population decreases have been reported in many areas of the Pallid Harrier's breeding range, particularly in the peripheral populations breeding west of the Ural River (Davygora and Belik 1994; Bukreev 1997). Trends of the Asian core subpopulations have been less well documented, although local declines have been noted in several areas (Bragin 2003; Davygora and Belik 1994). As a result, the global conservation status of this species is now classified as 'Near Threatened' (Collar et al. 1994). Population declines may be associated with breeding and wintering habitat degradation and reduced prey availability due to land-use changes, and/or high mortality rates during migration and on the wintering areas (Birdlife International 2003; Terraube 2010). However, it has been recently suggested that its vulnerable conservation status may be linked to its specialist foraging strategy (Terraube et al. 2011). Therefore, getting to grips with the way in which factors such as prey abundance, habitat and time of year influence breeding numbers and performance could greatly improve our understanding of Pallid Harrier population dynamics and our ability to effectively set conservation priorities within the core breeding areas of this species.

The specific objectives of this paper are: (1) to determine the numerical response of Pallid Harriers to local changes in vole numbers during the breeding season, as a prerequisite for assessing the influence of prey density on Pallid Harrier dynamics; (2) to evaluate whether Pallid Harrier density varies predictably at a local scale (indicating cyclic variation in prey), and asynchronously across adjacent areas (indicating between-area large-scale movements across years); (3) to determine how vole abundance, breeding habitat and timing of breeding (as a surrogate of the duration of the pre-breeding prospecting period) affect the breeding success of Pallid Harriers at a local scale.

Methods

Study area

We conducted fieldwork in the Naurzum National Nature Reserve and surrounding areas (hereafter referred as to "study area") in north-central Kazakhstan (Fig. 1; Kostanay

Oblast, 51°N, 64°E) in June 2000, June 2006, May–July 2007 and 2008, and early June to mid-July 2009. The study area, located at the southern limit of Siberian forests and northern limit of Eurasian steppes, is characterised by a mosaic of dry steppes, riverbeds, bushy areas and woodland patches (Katzner et al. 2003; Terraube 2010). We monitored an area of ca. 700 km² (we estimated survey area by assuming a visibility of 1 km from the network of accessible tracks that we regularly travelled within the overall area, which totalled ca. 350 km in length).

Additionally, we conducted raptor road censuses in the study area between 1997 and 2005, and also at a regional scale in more recent years (Fig. 1; see details below).

Local prey abundance

Small mammals such as voles exhibit strong inter-annual fluctuations in abundance in Kazakhstan (Bragin 2003; Davies et al. 2004). We estimated vole abundance directly in the study area in 2006 (in June) and 2007–2009 (from late May to early July), using an index based on the occurrence of fresh vole droppings. This index is correlated with estimates of vole abundance derived from trapping methods (Tapper 1979; Madders 2003). Twenty-five quadrats (25 × 25 cm) were randomly located in each of 11 (2006) and 24–25 (2007, 2008 and 2009) plots (each plot being a ca. 500 m² area located within the study site). Each quadrat was sampled for the presence (1) or absence (0) of fresh (less than 1 week old) vole faeces (moist and greenish in colour). Presence/absence scores were then summed across the 25 quadrats in each plot, and averaged across sampled plots, to obtain an index of vole abundance (Madders 2003). We located the plots in the main vegetation types present in the study area (dry steppes, sandy steppes, rye-grass (*Lolium* sp.) or wet steppes, steppe along rivers, hereafter called riverine steppe and agricultural areas). The position of each quadrat differed between assessments and was determined by walking 20 paces from the previous quadrat. In 2006, we did not sample rye-grass steppes. We did not quantify vole abundance in 2000, but we were able to estimate the vole abundance index from the relationships between our vole abundance index and the % of small mammals in the diet of Pallid Harriers (assessed through pellets collection and analysis, see Terraube et al. 2011 for further details) for the other four study years (vole index = 0.143 × [% small



Fig. 1 Location of study area (Naurzum; black dot) in north-central Kazakhstan (left) and regions of road censuses (right; each number and red area refers to a separate region). (Color figure online)

mammals] – 2.03; $R^2 = 0.958$; see Terraube et al. 2011). This relationship gave an estimated vole abundance index of 8 for the year 2000 (Terraube et al. 2011).

Pallid Harrier abundance

We located nests in the study area by following males carrying prey and locating where females landed after a food pass. During the first survey in 2000, we visited a total of 24 Pallid Harrier nests (out of 35 located) and five more Pallid Harrier broods were found after fledging. In June 2006, we found 46 Pallid Harrier nests and visited 45. During 2007, only 5 nests were located and 2 were visited; in 2008, we found and visited a total of 31 nests and in 2009, 10 nests (out of 12 located) were visited. The location of all nests and known pairs was recorded using a GPS. Nest location was subsequently plotted in a GIS (ArcView 3.2, ESRI Inc. and Redlands, CA). In all cases, we estimated Pallid Harrier breeding abundance in the study area as number of located nests in relation to survey effort (calculated as number of man-days in each study year, see Table 1).

E. and A. Bragin conducted roadside counts to assess the relative abundance of all raptor species in the steppe habitats of north Kazakhstan. From this data set, we extracted the Pallid Harrier sightings. This included roadside counts carried out in the Naurzum region (in an area larger than, and including, the study area: labelled as zone 4 in Fig. 1) over a 13-year period (1997–2009), as well as roadside counts in four other areas of steppe habitat in surrounding regions (labelled as zones 2, 3, 5 and 7–8 in Fig. 1) during a varying number of years, depending on survey areas (not all areas were surveyed for the whole time-period 1997–2009). During surveys, both observers scanned for raptors, while driving at 30–40 km/h along road transects, between sunrise and sunset (08:00–20:00), with regular stops to accurately identify species using 10×42 binoculars. All counts were made during the breeding season (from May to middle July), and in good weather conditions, with good visibility and light winds. All individuals seen perched or flying, within view on either side of the roads, were counted. The length of transects (measured using the vehicle odometer and road maps), totalled 23,832 km. Pallid Harrier survey data are presented as the number of birds observed per 100 km of road transects in a given area (Fig. 1) and year.

Estimation of Pallid Harrier breeding parameters

We categorised the vegetation around each nest we found into one of four main types (Terraube et al. 2009): (1) steppe (open areas with low vegetation, being dry or humid; this included also nests in abandoned agricultural areas), (2) lakes (reeds in lakes or temporary ponds, whether containing water or not), (3) riverine habitats (reeds along rivers), and (4) steppe-river (steppe vegetation but less than 50–100 m from rivers).

During each nest visit, we recorded clutch size or, if the nest contained nestlings, we measured wing-length to estimate chick age and hatching date. Nestling ages were estimated using wing-length growth curves for a similarly sized species (Hen Harrier *Circus cyaneus*; Terraube et al. 2009). Laying date was estimated directly (if the nest was visited during laying), or by subtracting 30 days from the estimated date of hatching (Terraube et al. 2009). Mean laying date for all years was 7 May \pm 16 days ($n = 111$ nests), but the laying period spanned over almost 2 months within each year and the distribution of onset of laying dates each year was bimodal, suggesting two distinct waves of arrival rather than a continuous variation in individual quality (Terraube et al. 2009). For analyses, we categorised each nest as “early” (if laying date was earlier than the observed average for each year) or “late” (if laying date was later than the annual average).

Table 1 Vole abundance indices and reproductive parameters of Pallid Harriers during the 5-year study in the Naurzum region (north-central Kazakhstan)

Year	2000	2006	2007	2008	2009
Vole index	[8.0] ^a	8.8 ± 8.1 (11)	0 ± 0 (25)	4.0 ± 5.1 (24)	1.2 ± 2.9 (25)
Vole ab. year class	High	High	Low	Interm.	Low
% Small mammals in diet	67.2	77.1	21.9	38.4	19.4
Survey effort (man-days)	52	57	104	94	79
Breeding pairs found	40	46	5	31	10
Breeding density ^b	0.77	0.81	0.05	0.33	0.15
Mean laying date (Julian days) (range; sample size)	31.3 ± 18.9 (10–71; 24)	38.3 ± 16.8 (11–64; 40)	42.9 ± 15.3 (25–59; 7)	35.4 ± 12.7 (7–55; 31)	50.4 ± 8.4 (35–60; 9)
Clutch size	5.7 ± 0.8 (12)	5.6 ± 1.3 (26)	4.0 ± 0.0 (2)	4.8 ± 0.7 (24)	3.5 ± 1.2 (6)
Hatching success	100 % (20)	83.9 % (31)	50 % (4)	90 % (30)	66.6 % (9)
Nesting success	96.6 % (29)	87.0 % (46)	0 % (5)	87.1 % (31)	30.0 % (10)
Fledged brood size	2.7 ± 1.7 (16)	3.2 ± 1.6 (10)	na	2.6 ± 1.3 (22)	2.0 ± 0 (1)

Sample sizes (in brackets) refer to number of nests. Data are given as means ± SD

^a Estimated data, see “Methods” section

^b Number of breeding pairs found/survey effort

We determined clutch size, fledged brood size (determined as the number of nestlings in successful nests at week 3), hatching success and nest failure for each nest. Hatching success was defined as 1 if at least one egg of the clutch hatched and as 0 if no egg hatched. Nest failure was defined as 1 if no young fledged and as 0 if at least one young fledged. Nest failure included clutch loss during incubation and post-hatching failure (i.e. brood loss through predation, chick death by starvation or parental abandonment).

During 2007–2009, all the nests we found were checked a minimum of three times to determine clutch size, brood size at 3 weeks and nesting success. In contrast, fieldwork in the first 2 years (2000 and 2006) covered only part of the breeding season and therefore the evaluation of breeding parameters was necessarily restricted and subject to some biases. For example, final clutch size was known for late breeders (which were still incubating eggs at the time of the first nest visit), but not for all early breeders (because some clutches had hatched before the first visit). In order to make sure that observed trends were not unduly influenced by such biases, we used only those nests for which the final clutch size was known. On the other hand, fledging success was not always known for late breeders (which had not fledged by the time of our last visit). When a nest had not been followed until fledging, we approximated fledged brood size as the brood size at last visit (if the last visit had occurred when the nestlings were at least >15 days old). If the last visit had occurred with very small nestlings, we excluded that nest from this analysis. Thus, fledged brood size in these 2 years (2000 and 2006) may be overestimated. However, most of the nestling mortality in harriers occurs in the first 2 weeks after hatching (Castaño 1997; Arroyo 2002; Redpath et al. 2002), and nestling mortality is likely to be small particularly in high food abundance years (such as 2000 and 2006, Terraube et al. 2009), so we believe this bias is likely to be small. Sample size varied among different models according to the information collected and available from each nest. We are aware that using different datasets to test different models could be a potential source of bias, but we preferred to do so in order to use all available information, as using only nests for which all information was available would strongly reduce sample size, and other types of biases may arise.

Fieldwork was conducted under permit and according to Kazakh guidelines for the study of animals in the field.

Statistical analyses

To identify the factors linked with variations in vole abundance in our study area, we used generalized linear models (GLMs); vole abundance estimate per plot (the number of quadrats with fresh droppings) was modelled using a log-link function with Poisson errors. The model included two categorical variables: habitat type (5 classes: dry steppes, sandy steppes, rye-grass, riverine areas and agricultural areas) and year, as well as the interaction between habitat and year.

To analyse our time series of Pallid Harrier abundance, we used the PAST software (Hammer and Harper 2006) and performed a spectral analysis to search for periodicity in the abundance fluctuations.

To analyse numerical responses by harriers, we used the number of Pallid Harrier nests found each year divided by the survey effort (measured as the sum of man-days of survey) to derive an index of Pallid Harrier density. Thereafter, we fitted the numerical response of Pallid Harriers to a log-transformed vole density index using a GLM, with a Gaussian error distribution and an identity link function.

To identify the factors linked with variations in breeding success in our study population, we also used GLMs. Clutch size and fledged brood size were modelled using a log-

link function with Poisson errors, while hatching and nesting success were modelled as binomial responses and fitted with a logistic link function. We evaluated models that included the following explanatory variables: vole abundance as a continuous variable; two categorical variables: habitat type (steppe, lake, riverine habitats, or river-steppe, as defined above) and timing of breeding (“early” or “late”, as defined above); as well as the two-way interaction between these last variables. However, binomial models with two-way interactions did not converge (probably because of a lack of data in each of the categories) so we removed the interactions from these models. Our models evaluating nest or hatching success did not account for nest exposure time. Thus, results may be biased depending on the stage of nest finding, particularly if this varied according to explanatory variables (for instance, if there is a higher likelihood of missing failed nests according to habitat type or laying date). In order to evaluate this potential source of bias, we reported on the proportion of nests found at each nest stage (incubation, young, i.e. <10-days old, chicks or old, >9 days old, chicks) in Table 4. Model selection was performed following a manual backward stepwise elimination procedure, by excluding non-significant explanatory factors, starting with interaction, until the model contained only significant factors.

All GLMs were implemented using the GENMOD procedure in SAS 9.1 and all values are presented as means \pm SD.

Results

Vole and Pallid Harrier abundance

Vole abundance in the study area varied greatly between study years, ranging from 0 to 8.8 (Table 1). Variation in vole abundance was significantly explained by year ($\chi^2_3 = 283.34$; $P < 0.0001$), habitat ($\chi^2_4 = 154.59$; $P < 0.0001$), and their interaction ($\chi^2_{11} = 61.80$; $P < 0.0001$). In 2006 and 2008, when voles had respectively high and intermediate abundance, vole indices were present in almost all habitat types, although highest abundances were in tall and dense herbaceous vegetation along the rivers, where voles also concentrated in lower abundance years (Table 2). In 2008 only, highest vole abundances were found in rye-grass steppes.

The relationship between the indices of Pallid Harrier abundance (i.e. number of Pallid Harrier nests found divided by survey effort) and vole abundance index for 2006–2009 was highly significant ($\chi^2_1 = 17.76$; $P < 0.0001$), with vole abundance explaining 99 % of the variance in observed Pallid Harrier density in those 4 years (Fig. 2).

Table 2 Vole abundance estimates in relation to habitat

	2006	2007	2008	2009
Dry steppe	8.7 \pm 7.5 (3)	0.0 \pm 0.0 (10)	3.0 \pm 2.8 (7)	0.2 \pm 0.4 (5)
Riverine steppe	14.2 \pm 7.4 (5)	0.0 \pm 0.0 (4)	6.3 \pm 5.5 (3)	5.8 \pm 4.4 (5)
Rye-grass	No data	0.0 \pm 0.0 (5)	11.2 \pm 4.8 (5)	0.4 \pm 0.5 (5)
Agricultural areas	0.0 \pm 0.0 (1)	0.0 \pm 0.0 (3)	0.8 \pm 1.8 (5)	0.0 \pm 0.0 (5)
Sandy steppe	4.0 \pm 0.0 (2)	0.0 \pm 0.0 (2)	0.0 \pm 0.0 (4)	0.0 \pm 0.0 (5)
Total	8.8 \pm 8.1 (11)	0 \pm 0 (25)	4.0 \pm 5.1 (24)	1.2 \pm 2.9 (25)

Sample sizes (in brackets) refer to number of plots. Data are given as means \pm SD

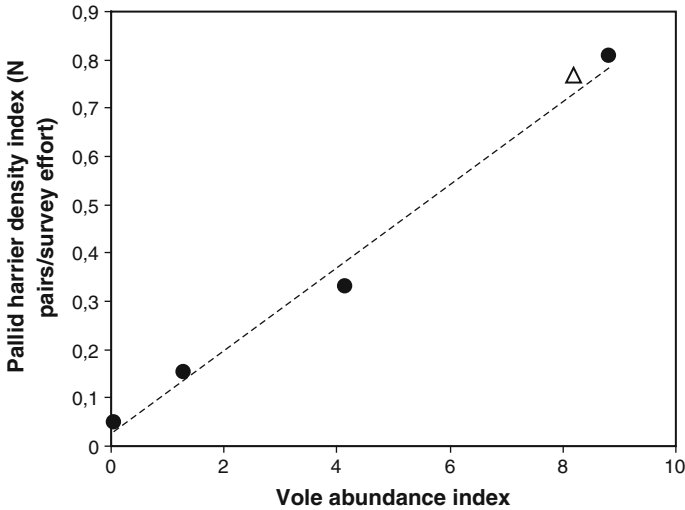


Fig. 2 Pallid Harrier breeding density as a function of vole abundance in the Naurzum region. For 2000 (black triangle), vole abundance was not measured but estimated from pellet data (see “Methods” section). When also including this estimation for 2000, the relationship between vole abundance and observed Pallid Harrier density was as follows: [Pallid Harrier density] = (0.0859 × [vole index]) + 0.0269

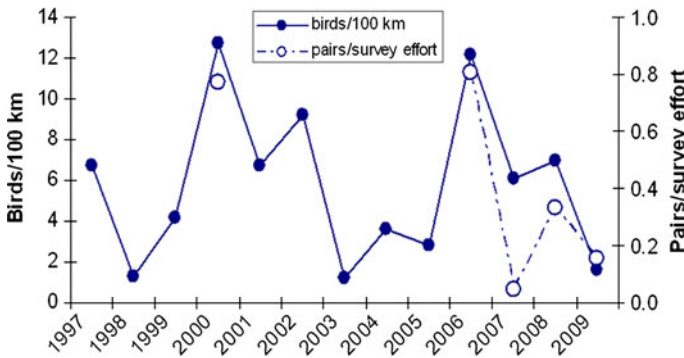


Fig. 3 Time series of Pallid Harrier density (closed symbols; number of birds encountered per 100 km of road) in the Naurzum region from 1997 to 2009 (left) and spectral analysis conducted on this time series (right). Superimposed to the time series (open symbols) is the breeding density (number of pairs/survey effort) in the study area in the study years (2000 and 2006–2009)

Pallid Harrier relative abundance estimated from road censuses in the Naurzum region showed strong interannual variations during the 13-year period of the survey (Fig. 3). A spectral analysis conducted on these data show a peak frequency at 0.173, which would be indicative of a c. 6-year period. Although the power at this peak frequency did not reach statistical significance ($0.05 < P < 0.10$), our short-time series is consistent with a 6 year-period cycle in Pallid Harrier abundance. Within our study period, there were two marked peaks in harrier abundance (2000 and 2006), and 3 years of very low harrier density (1998; 2003 and 2009, Fig. 3).

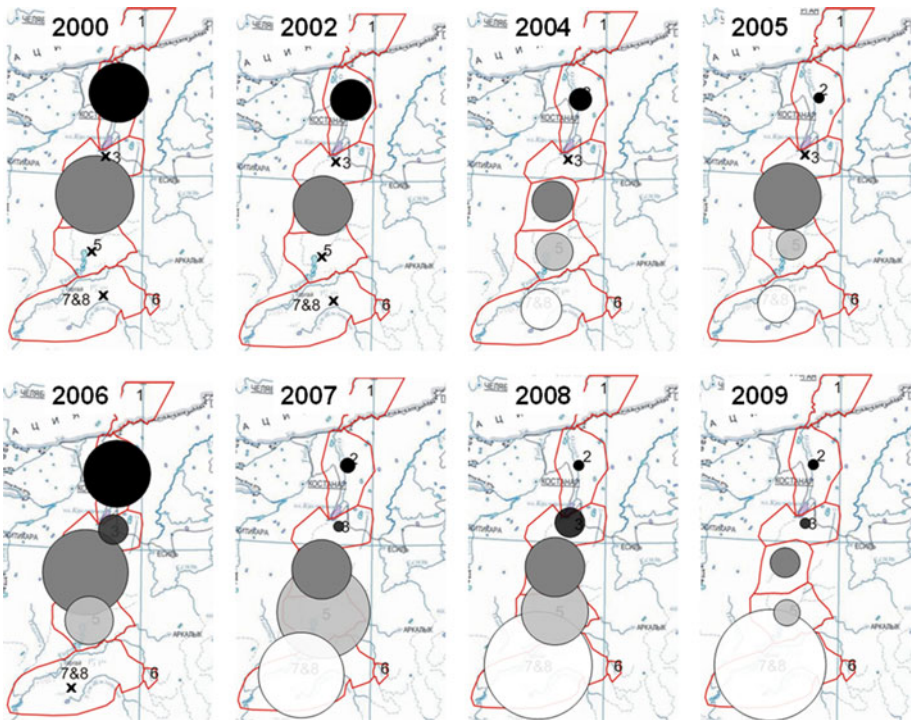


Fig. 4 Spatiotemporal variation in relative abundance (birds/100 km) of Pallid Harriers in five sites in north Kazakhstan. Regions where road censuses were carried out where 2, 3, 4, 5 and 7–8 in Fig. 1. Data from each of these regions is represented with a different colour (*black* for region 2, *dark grey* for 3, *medium grey* for 4, *light grey* for 5 and *white* for 7–8). An “X” represents lack of data for a region in a given year. Circle size is proportional to Pallid Harrier density. (Color figure online)

The spatiotemporal variation in the abundance index of Pallid Harriers indicates that year-to-year variations within a site were not necessarily reflected across sites, suggesting a regional redistribution of harriers between years (Fig. 4).

Factors driving Pallid Harrier breeding success

Clutch size was positively related to vole abundance and was higher for early than for late breeders, but was not related to habitat type (Table 3).

Hatching success was also significantly and markedly higher for early breeders than for late breeders, but neither habitat type nor vole abundance had a significant influence on this parameter (Table 3).

Nest failure was significantly affected by vole abundance and habitat type (Table 3): it was higher when voles were scarce, and for breeding pairs nesting in or along rivers than for pairs breeding in lakes and steppe habitats (Table 3).

Fledged brood size varied in relation to vole abundance and habitat type, and also in relation to their interaction, but no effect of breeding timing was found once controlling for the other variables (Table 3). Fledged brood size increased with increasing vole abundance, but both the intercept and the slope of this relationship varied among habitats (as evidenced by the interaction between vole abundance and habitat, Table 3). Overall,

Table 3 Results of the final GLM models showing the variables that influence variations in the breeding parameters of Pallid Harriers

	Vole abundance	Habitat type	Timing	Vole abundance * habitat type
Clutch size	$\chi^2_1 = 43.21; P = 0.0001$ Estimate: 0.30 ± 0.05		$\chi^2_1 = 9.43; P = 0.002$ Estimate: Early: 1.18 ± 0.14 Late: 1.03 ± 0.09	
Hatching success			$\chi^2_1 = 13.17; P = 0.0003$; Estimate: Early: 3.13 ± 0.24 Late: 0.59 ± 0.39	
Fledged brood size	$\chi^2_1 = 6.91; P = 0.0009$; Estimate: 1.04 ± 0.61	$\chi^2_3 = 9.55; P = 0.048$ Estimate: Lake: 0.35 ± 1.33 River: 3.30 ± 1.67 Steppe: 1.51 ± 0.72 Steppe-river: 0.85 ± 1.25		$\chi^2_4 = 8.25; P = 0.041$; Estimate: Vole ab. × lake: 0.46 ± 0.89 Vole ab. × river: 2.00 ± 1.01 Vole ab. × steppe: 0.24 ± 0.73 Vole ab. × steppe-river: 1.04 ± 0.61
Nest failure	$\chi^2_1 = 26.13; P = 0.0001$; Estimate: 3.29 ± 0.89	$\chi^2_3 = 14.30; P = 0.025$; Estimate: Lake: 3.19 ± 1.25 River: 5.73 ± 1.78 Steppe: 2.28 ± 1.70 Steppe-river: 4.70 ± 1.86		

Estimates are given as means ± SE

fledged brood size was higher in rivers and lakes when voles were abundant, but was higher in steppes when they were scarce.

Discussion

We found that in Pallid Harriers: (i) local breeding numbers show a strong numerical response to vole density; (ii) regional abundance greatly varied among years, possibly with a 6-year period, and apparently asynchronously among contiguous regions and (iii) breeding success depends on vole abundance, and also on timing of breeding and breeding habitat type: late nesters laid smaller clutches and had higher probabilities of failing, particularly if nesting in riverine habitats (which are used more frequently as the season progresses). Below we discuss these findings and their implications for our understanding of the ecology and conservation needs of nomadic predator specialists.

Numerical response of Pallid Harrier to vole abundance variations

The strong numerical response observed at the local scale, in addition to the changing patterns of relative abundance of Pallid Harriers at the regional scale, are consistent with high mobility and a nomadic breeding strategy (Ferguson-Lees and Christie 2001; Terraube et al. 2011). Data from satellite tracking has confirmed both of these traits in Pallid Harriers showing that they undertake prospecting trips up to 3,000 km between returning from their wintering areas and settling on their breeding grounds, lasting up to 3 weeks (Terraube 2010) and have very large breeding dispersal distances (mean 652 ± 271 kms; Terraube 2010 and unpublished data). This suggests that, during the breeding period, Pallid Harrier is a true nomadic, rodent-specialist raptor. The large-scale variations in breeding density we found could be due to inter-annual movements of Pallid Harriers between different breeding areas in response to large-scale fluctuations in vole densities.

The numerical response observed between breeding harriers and voles (Fig. 2) suggests that Pallid Harrier abundance is tightly correlated with vole abundance at the local scale (see Sundell et al. 2004, for similar assumptions about rodent-specialist raptors in northern ecosystems). Assuming this is the case, the cyclical pattern in breeding Pallid Harrier numbers, suggested by our relatively short-time series, raises the possibility of a similar cycle in vole populations, with a 6 year period (Fig. 3) and little synchrony between neighbouring regions (Fig. 4). This should be confirmed with longer time series of vole abundance (a 13-year time series is too short for confirming a 6-year period cycle as it can only include two peaks or lows), also looking at larger scales. Studies on microtine dynamics in Scandinavia and western Europe at similar latitudes have shown clear 3–4 years cycles (Korpimäki and Norrdhal 1991; Salamolard et al. 2000; Gilg et al. 2006; Lambin et al. 2006) and greater spatial synchrony of vole fluctuations (Spitz 1977; Bowman et al. 2000; Huitu et al. 2005), also reflected in the patterns of variation in the abundance of vole specialist raptors and other predators in those areas.

The patterns of rodent density variations observed in the study area might result from the interaction of several mechanisms. Two climatic parameters, namely the amount of rainfall and temperature are known to affect reproduction and survival of small rodents (Koontz et al. 2001). Additionally, climatic variables may interact with density dependent processes, as the interaction between density and mean temperatures has been shown to strongly influence vole survival (Goswami et al. 2011). At a more local scale, grazing

intensity has been also shown to influence vole densities in Central-Asian steppes (Zhang et al. 2003).

Finally, predation has an important role in shaping vole population dynamics and often can limit the population growth of voles (Sundell 2006). Steppes of north-Kazakhstan harbour a highly diverse predator guild preying potentially on small mammal species, including specialist (Pallid Harriers, Short-eared Owls *Asio flammeus*) and generalist predators (two fox species, mustelids and a diverse raptor community). Therefore, the role of predation interacting with the previous cited mechanisms cannot be excluded in explaining the variation in rodent densities observed.

Factors linked with variations in Pallid Harrier breeding parameters

Breeding success in Pallid Harriers was affected by vole density, breeding habitat and breeding timing and the interactions between these variables. We showed the dependence of Pallid Harrier on voles for breeding, with key parameters such as clutch size, fledged brood size and nesting failure being strongly affected by vole abundance. Small rodents dominate the diet of Pallid Harriers, and vole abundance strongly affects their hunting efficiency (Terraube et al. 2011). Considering the level of specialization of this species, the strong influence of vole abundance on almost all breeding parameters, is unsurprising and was probably mediated through variations in the condition of breeders or nestling starvation (Newton 1979). In addition, nest predation risk was also higher in low vole years, probably as a result of harrier nestlings becoming alternative prey for other predators (e.g. foxes) that prey on voles when these are abundant (authors' unpub. data).

Interestingly, breeding habitat type also influenced nest failure and fledged brood size, after taking into account vole abundance. The influence of habitat on reproductive output could be driven by (i) inter-habitat variation in prey abundance or availability; (ii) vegetation structure (height or density) around the nest influencing local micro-climate conditions; and (iii) inter-habitat differences in predation risk. Of the five habitats sampled for voles, riverine steppes held the highest densities of voles (Table 2). We might therefore expect this habitat to be selected by nesting Pallid Harriers, because of the advantages to central-place foragers of nesting near areas with high prey density (Orians and Pearson 1979). The large size of broods fledged from this habitat when voles were abundant also implies that riverine steppe is high quality with regard to food supply. However, breeding failure was highest in nests located in riverine habitats or in steppe vegetation near rivers, possibly as a result of higher predation rates by mammalian predators such as foxes and mustelids, particularly during incubation (Terraube et al. 2009). This result should however be taken with caution because of a possible bias in the nest stage discovery of nests in this habitat (Table 4), as a higher proportion of nests were discovered in this habitat during incubation, therefore potentially over-estimating nesting success in other habitats if nests failed during incubation were unnoticed. Given their corridor-like nature in otherwise homogeneous steppe habitats, the riverine habitats may be used as regular foraging routes by terrestrial predators, potentially resulting in a higher predation rate (Terraube et al. 2009). In contrast, in lakes, nests might be less accessible for terrestrial predators.

Nesting habitat preferences also varied over the course of the breeding season, with early breeders using all habitats while late breeders favoured riparian areas. In addition, breeding habitat preference varies throughout the season, as early breeders used all habitats whereas late breeders favoured riverine habitats for nesting (Terraube et al. 2009). Microclimate at the nest site can explain differences in breeding success through the influence of temperature on hatching success and chick survival (Öst et al. 2008). Climate

Table 4 Variation in the percentage of nests found during the three stages of the breeding cycle (incubation; young chicks, i.e. <10 days old; or old chicks, i.e. >9 days old) according to the main explanatory variables (year, habitat type, breeding timing and vole abundance)

Breeding stage	% Nests found during		
	Incubation	Young chicks	Old chicks
By year			
2000	51.7	27.6	20.7
2006	56.8	36.4	6.8
2007	50.0	50.0	0.0
2008	61.3	35.5	3.2
2009	66.7	22.2	11.1
By habitat type			
Lake	57.9	5.3	36.8
River	75.6	4.9	19.5
Steppe	41.0	17.9	41.0
Steppe-river	52.9	0.0	47.1
By breeding timing			
Early	32.3	16.9	50.8
Late	88.0	0.0	12.0
By vole abundance years			
High	54.8	12.3	32.9
Interm.	61.3	3.2	35.5
Low	61.5	7.7	30.8

in Central Asia is strongly continental with very low winter temperatures (between $-20/-40$ °C) and short, very hot summers (up to 40 °C). Very high temperatures are particularly frequent in the study area during the month of June (authors pers. obs; <http://www.worldclimate.com>), corresponding to the laying period of late-breeding Pallid Harriers. This could lead these birds to favour shaded nest sites in riverside reedbeds, which are among the only areas providing such protection from the sun in steppe landscapes. This could explain the strong selection of riverine habitat in our study area by late breeders, despite the association of this habitat with high nest predation rates. Reeds growing in riverbeds are the only habitat providing this type of protection and could explain the strong selection of this habitat in our study area in late breeders, maybe in a counter-selective pattern as these habitats are associated with higher predation risk (Terraube et al. 2009).

Finally, timing of breeding also influenced breeding output, due to an effect on clutch size and hatching success (mainly through higher predation rates in the breeding habitats selected late in the season). While the effect of the timing of breeding on clutch size is a priori unlikely to be affected by the stage at which nests were found, the same might not be true for hatching success. Because we found fewer early nests than late nests during incubation (Table 4), we may have missed some failed early nests, and thereby overestimated hatching success in early breeders. Hence, the relative differences in terms of hatching success should be taken with caution. A seasonal decrease in clutch size and overall reproductive success has been reported in numerous bird species and has been associated with higher parental quality of early-breeding birds, and decreased in environmental quality through the breeding season, or both (Arnold et al. 2004). However, in the case of Pallid Harriers the onset of laying occurs over more than 2 months, and the distribution of lay dates throughout the season is bimodal, suggesting that there may be

multiple factors influencing timing of breeding (Terraube et al. 2009). Additionally, the lack of an obvious negative relationship between lay date and either brood size or nest success suggests that variation in breeding output between both groups is not exclusively due to variation in individual quality.

We propose that the observed pattern could be a consequence of intrapopulation differences in pre-breeding prospecting strategy. A positive relationship between breeding dispersal distance and the reproductive costs of dispersal (sometimes influenced by the breeding individual's quality) has been shown by several studies (Danchin and Cam 2002; Cam et al. 2004; but see Doligez and Part 2008). Pallid Harriers undertake large breeding dispersal movements, associated with a long prospecting period after birds arrive from their wintering areas (Terraube 2010). Birds returning to Kazakhstan, prospect for 21 ± 15 days, and travel $1,720 \pm 753$ km during this time ($n = 3$ females and 4 reproductive events; unpublished data). This inter-individual variation in prospecting duration and distance travelled suggests that some individuals might be better than others at quickly locating high vole abundance areas for breeding. A possible explanation for the decrease in clutch size among late breeders is that long prospecting period incurs a fitness cost in terms of body condition due to the distance travelled.

Conclusions

Breeding success of Pallid Harriers depends primarily on several parameters; vole abundance (the preferred prey), but also on local habitat heterogeneity and on timing of breeding. The latter is likely to be the consequence of how long it takes individuals to find good breeding areas, with a potential cost of long prospecting periods (Newton 2003, 2007).

Second, our data suggest that vole abundance in Kazakhstan fluctuates cyclically, possibly with a 6-year period, but asynchronously at a large spatial scale. Such a long period and pattern of variation may make it potentially difficult for harriers to accurately predict when and where the next vole outbreaks will occur. A lack of synchronicity at the regional scale implies that it should be possible for a returning harrier to find good breeding areas within a few hundred kilometres of a previous breeding place that happens to have no voles upon arrival from the wintering grounds. However, if vole dynamics change, the efficiency of this strategy might also change.

In Central Asia, the abundance of small rodents varies with climatic conditions and grazing intensity, the key factor determining habitat quality for rodents being grassland structure (Zhang et al. 2003). Gilg et al. (2009) showed also that climate change very robustly predicts reduced cyclicality and reduced peak densities of lemmings.

Climate change in Central Asia is expected to increase rainfall stochasticity and increase summer heat in the southernmost areas (Lioubimtseva and Henebry 2009), with warmer and wetter conditions at the northern latitudes (Yu et al. 2003). This would increase rangeland productivity and as a consequence cattle numbers, and allow further agricultural intensification across the northernmost areas (Joyner et al. 2010; and see Baker et al. 1993 for a study conducted at similar latitudes to Kazakhstan). Changes in grazing and agricultural patterns in the northern part of the Pallid Harrier's breeding range in conjunction with increasing aridity in the southern areas would have a strong impact on the steppe vegetation and are likely to have impact on the structure of steppe vegetation and, consequently, on vole dynamics. Agriculture intensification is also known to reduce small rodent densities (Butet and Leroux 2001; Jacob 2003; Aschwanden et al. 2007) and

Kazakhstan has experienced a strong economic increase in recent years, associated with agricultural intensification and a net recent growth in livestock numbers after years of decrease (Bragin 2003). Climate and land-use changes could act simultaneously on the vegetation structure and composition of Central-Asian steppes through a general process of pasture degradation. This could increase the number of sites showing simultaneously low vole densities, implying that Pallid Harriers would need longer prospecting phases to find good breeding areas, with associated reductions in breeding success, which could negatively influence the long-term viability of the core Kazakh and Siberian Pallid Harrier populations.

The implementation of agri-environment schemes to protect traditional use of the steppes (extensive pastoralism) could help conserve high densities of small mammals, through for example the conservation of corridors from source habitats in the riverine steppe habitats, where grazing activity could be restricted. This appears essential to the large-scale conservation of Pallid Harriers in the remaining core populations.

Acknowledgments We are grateful to Robert Stakim, Jeff Watson, Becky Wills, Jesús T. García and Thomas Cornulier for help with data collection. Becky Wills also acted as a translator in 2000, and Ainur Akmetova helped with translations and logistics in 2006. We are also very thankful to Todd Katzner for assistance in setting up the project and help with the subsequent fieldwork logistics and to Natural Research Ltd, for funding this research project. We are indebted to the current director of the Naurzum Nature Reserve, Muttakov Bagitjan Zhakezhanovich, the Deputy Director, Zeinelova Maria Alexandrova and all the staff of the Reserve. We also thank Mark Wilson and an anonymous referee for comments on the manuscript. We dedicate this work to the late M. Madders.

References

- Angerbjörn A, Tannerfeldt M, Erlinge S (1999) Predator–prey relationships: arctic foxes and lemmings. *J Anim Ecol* 68:34–49
- Arnold JM, Hatch JJ, Nisbet ICT (2004) Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *J Avian Biol* 35:33–45
- Arroyo B (2002) Sex-biased nestling mortality in the Montagu's harrier *Circus pygargus*. *J Avian Biol* 33:455–460
- Aschwanden J, Holzgang O, Jenni L (2007) Importance of ecological compensation areas for small mammals in intensively farmed areas. *Wild Biol* 13:150–158
- Baker BB, Hanson JD, Bourdon RM, Eckert JB (1993) The potential effects of climate change on ecosystem processes and cattle production on US Rangelands. *Clim Chang* 25:97–117
- Berthold P (2001) Bird migration: a general survey. Oxford University Press, Oxford
- Birdlife International: International Action plan for the Pallid harrier (*Circus macrourus*). Convention on the conservation of European wildlife and natural habitats. Standing committee. 23rd Meeting. Strasbourg, 1–4 Dec 2003
- Bowman J, Forbes G, Dilworth T (2000) The spatial scale of variability in small mammals populations. *Ecography* 23:328–334
- Bragin EA (2003) Osobennosti rasprostraneniya, chislennosti i nekotorye cherty ekologii stepnogo lunya (*Circus macrourus*) v Kustanaiskoi oblasti. Distribution, number and some features of ecology of the Pallid harrier (*Circus macrourus*) in Kustanai region/Selevinia, pp 145–149 (in Russian)
- Brommer JE, Pietiäinen H, Ahola K, Karell P, Karstinen T, Kolunen H (2010) The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Glob Change Biol* 16:577–586
- Bukreev SA (1997) Ornitogeografiya i zapovednoe delo Turkmenistana [Ornithogeography and reserve protection in Turkmenistan]. M, CODP SoES 160
- Butet A, Leroux A (2001) Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biol Conserv* 100:289–295
- Cam E, Monnat JY, Royle JA (2004) Dispersal and individual quality in a long-lived species. *Oikos* 106:723–736
- Caro T (2005) Antipredatory defences in birds and mammals. University of Chicago Press, Chicago

- Castaña JP (1997) Fenología de puesta y parámetros reproductivos en una población de aguilucho cenizo en el campo de Montiel. *Ardeola* 44:51–60
- Clavel J (2007) Spécialistes et généralistes face aux changements globaux: Approches comportementales et évolutives. PhD Thesis, Université Pierre et Marie Curie, Paris
- Collar NJ, Crosby MJ, Stattersfield AJ (1994) Birds to watch 2. The world list of threatened birds. BirdLife International, Cambridge
- Danchin E, Cam E (2002) Can non-breeding be a cost of breeding dispersal? *Behav Ecol Sociobiol* 51:153–163
- Davies S, Begon M, De Bruyn L, Ageyev VS, Klassovskiy NL et al (2004) Predictive thresholds for plague in Kazakhstan. *Science* 304:736–738
- Davygora AV, Belik VP (1994) The pallid harrier *Circus macrourus* as an endangered species in the Palearctic. In: Meyburg B-U, Chancellor RD (eds) Raptor conservation today: proceedings of the IV world conference on birds of prey and owls. WWGBP/The Pica Press, Bodmin, Cornwall, pp 93–96
- Doligez B, Part T (2008) Estimating fitness consequences of dispersal: a road to “know-where”? Non-random dispersal and underestimation of disperser’ fitness. *J Anim Ecol* 77:1199–1211
- Ferguson-Lees J, Christie DA (2001) Raptors of the world. Helm, London
- Gilg O, Sittler B, Sabard B, Hurstel A, Sané R, Delattre P, Hanski I (2006) Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:196–213
- Gilg O, Sittler B, Hanski I (2009) Climate change and cyclic predator–prey population dynamics in the high Arctic. *Glob Change Biol* 15:2634–2652
- Goswami VR, Getz LL, Hostetler JA, Ozgul A, Oli MK (2011) Synergistic influences of phase, density and climatic variation on the dynamics of fluctuating populations. *Ecology* 92:1680–1690
- Hakkarainen H, Koivunen V, Korpimäki E (1997) Reproductive success and parental effort of Tengmalm’s owls: effects of spatial and temporal variation in habitat quality. *Ecoscience* 4:35–42
- Hammer Ø, Harper DAT (2006) Paleontological data analysis. Blackwell, Oxford
- Hörnfeldt B, Hipkiss T, Eklund U (2005) Fading out of vole and predator cycles? *Proc R Soc Lond B* 272:2045–2049
- Huitu O, Lacksonen J, Norrdhal K, Korpimäki E (2005) Spatial synchrony in vole population fluctuations—a field experiment. *Oikos* 109:583–593
- Jacob J (2003) Short-term effects of farming practices on populations of common voles. *Agric Ecosyst Environ* 95:321–325
- Joyner TA, Lukhnova L, Pazilov Y, Temiralyeva G, Hugh-Jones ME et al (2010) Modeling the potential distribution of *Bacillus anthracis* under multiple climate change scenarios for Kazakhstan. *PLoS ONE* 5:e9596
- Julliard R, Jiguet F, Couvet D (2004) Common birds racing global changes: What makes a species at risk? *Glob Change Biol* 10:148–154
- Katzner T, Bragin E, Knick S, Smith A (2003) Coexistence in a multispecies assemblage of eagles in central Asia. *Condor* 105:538–551
- Klopfer PH, Ganzhorn JU (1985) Habitat selection: behavioural aspects. In: Cody ML (ed) Habitat selection in birds. Academic, New York
- Koontz TL, Shepherd UL, Marshall D (2001) The effects of climate change on Merriam’s kangaroo rat, *Dipodomys merriami*. *J Arid Environ* 49:581–591
- Korpimäki I, Norrdhal K (1991) Numerical and functional responses of kestrels, short-eared owls and long-eared owls. *Ecology* 72:814–826
- Lambin X, Bretagnolle V, Yoccoz NG (2006) Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? *J Anim Ecol* 75:340–349
- Lioubimtseva E, Henebry GM (2009) Climate and environmental change in arid and central Asia: impacts, vulnerability and adaptations. *J Arid Environ* 73:963–977
- Madders M (2003) Hen harrier *Circus cyaneus* foraging activity in relation to habitat and prey. *Bird Study* 50:55–60
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14:450–453
- Møller AP (1994) Sexual selection and the barn swallow. Oxford University Press, Oxford
- Newton I (1979) Population ecology of raptors. T & AD Poyser Ltd., Berkhamsted
- Newton I (2003) The role of natural factors in the limitation of bird of prey numbers: a brief review of the evidence. In: Thompson DBA, Redpath S, Fielding AH, Marquiss M, Galbraith CA (eds) Birds of prey in a changing environment. Scottish Natural Heritage, pp 5–23
- Newton I (2007) Irregular migrations: owls, raptors and waterfowl. In: The migration ecology of birds. Academic, Amsterdam

- Nielsen OK (1999) Gyrfalcon predation on ptarmigan: numerical and functional responses. *J Anim Ecol* 68:1050–1304
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn BJ, Stairs GH, Mitchell RD (eds) *Analysis of ecological systems*. Ohio State University Press, Columbus, pp 155–177
- Öst M, Wickman M, Matulionis E, Steele B (2008) Habitat-size specific clutch size and cost of incubation in eiders reconsidered. *Oecologia* 158:205–216
- Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci USA* 97:121144–121148
- Redpath SM, Arroyo BE, Etheridge B, Leckie F, Bouwman K, Thirgood SJ (2002) Temperature and hen harrier productivity: from local mechanisms to geographical patterns. *Ecography* 25:533–540
- Salamolard M, Butet A, Leroux A, Bretagnolle V (2000) Response of an avian predator to variations in prey density at temperate latitude. *Ecology* 81:2428–2441
- Shultz S, Bradbury RB, Evans KL, Gregory RD, Blackburn TM (2005) Brain size and resource specialization predict long-term population trends in British birds. *Proc R Soc Lond* 272:2305–2311
- Spitz F (1977) Le campagnol des champs (*Microtus arvalis*) en Europe. *Bull OEP* 7:165–175
- Sundell J (2006) Experimental tests of the role of predation in population dynamics of voles and lemmings. *Mam Rev* 36:107–141
- Sundell J, Huitu O, Henttonen H, Kaikusalo A, Korpimäki E, Pietiäinen H, Saurola P, Hanski I (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole eating avian predators. *J Anim Ecol* 73:167–178
- Tannerfeldt M, Angerbjörn A (1996) Life history strategies in a fluctuating environment: establishment and reproductive success in the arctic fox. *Ecography* 19:209–220
- Tapper F (1979) Effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. *J Anim Ecol* 48:603–617
- Terraube J (2010) Integrating foraging strategies, spatial movement patterns and reproductive success: implications for the conservation of sympatric avian predators. PhD Thesis, University of Castilla-La-Mancha
- Terraube J, Arroyo B, Mougeot F, Madders M, Watson J, Bragin EA (2009) Breeding biology of the pallid harrier (*Circus macrourus*) in north-central Kazakhstan: implications for the conservation of a near-threatened species. *Oryx* 43:104–112
- Terraube J, Arroyo B, Madders M, Mougeot F (2011) Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos* 120:234–244
- Terraube J, Mougeot F, Cornulier T, Verma A, Gavrillov A, Arroyo B (2012) Broad wintering range and intercontinental migratory divide within a core population of the near threatened pallid harrier. *Divers Distrib* 18:401–409
- Walsberg GE (1985) Physiological consequences of microhabitat selection in birds. In: Cody ML (ed) *Habitat selection in birds*. Academic, New York, pp 389–413
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–69
- Yu F, Price KP, Ellis J, Peijun S (2003) Response of seasonal vegetation development to climatic variations in eastern central Asia. *Remote Sens Environ* 87:42–54
- Zhang Z, Pech R, Davis S, Dazhao S, Xinrong W, Wenqin Z (2003) Extrinsic and intrinsic factors determine the eruptive dynamics of Brandt's voles *Microtus brandti* in Inner Mongolia, China. *Oikos* 100: 299–310