

1 **Short title:** Conservation of a nomadic specialist predator

2 **Title: Ecological factors influencing the breeding distribution and success**  
3 **of a nomadic, specialist predator**

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1 **Abstract**

2 Ecological specialization can explain the declining status of many species in the face of  
3 current global changes. Amongst specialists, nomadic predators present conservation  
4 biologists with many challenges, mainly because of the difficulty of studying highly mobile  
5 individuals over time and across very large areas. For these species, the relative influence  
6 of prey abundance, habitat heterogeneity and arrival time at the breeding grounds on  
7 breeding parameters remains poorly understood. We studied the factors influencing  
8 variation in breeding numbers and performance of a declining nomadic specialist raptor, the  
9 Pallid Harrier *Circus macrourus*, in north-central Kazakhstan. During a 5-year period, we  
10 recorded large inter-annual variation in vole abundance in the main study area, and  
11 differences between habitats. We also recorded a strong numerical response of breeding  
12 Pallid Harriers to inter-annual changes in local vole abundance. From a 13-year dataset on  
13 breeding harriers in the same area, harrier numbers appeared to vary cyclically, with an  
14 interval between peaks of approximately 6 years. At a broader, regional scale, variations in  
15 Pallid Harrier abundance appeared asynchronous, suggesting a regional redistribution of  
16 harriers between years. Reproductive success depended on local vole abundance, but also  
17 on timing of breeding and nesting habitat. Clutch size, nest success and fledged brood size  
18 increased with vole abundance. Late breeders had smaller clutches and apparently lower  
19 hatching rates than early ones, possibly as a result of the interplay between their probable  
20 poorer body condition and habitat-specific variation in predation rates. In true nomadic  
21 specialist predators, such as Pallid Harriers, breeding success may therefore depend on a  
22 complex interplay between spatial variation in prey abundance, habitat composition and  
23 timing of breeding attempts. One of the factors influencing the start of breeding is the  
24 length of time taken to prospect between different breeding sites, which in turn may depend  
25 on the predictability of spatial and temporal variation in vole abundance. These results have

1 important conservation implications, as changes in climate and habitat could affect spatial  
2 and temporal variations in vole abundance, with possible consequences for timing of  
3 breeding, food availability and, ultimately, the reproductive success of this declining  
4 nomadic predator.

5

6 **Keywords:** nomadic predator, breeding parameters, prey abundance, habitat composition,  
7 global changes, conservation, Kazakhstan, *Circus macrourus*;

8

9

# 1 **Introduction**

2

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

15

16 Understanding the factors determining variation in breeding numbers and performance is  
17 crucial to the effective management and conservation of many species. Despite being  
18 highly mobile, nomadic specialist predators are particularly sensitive to changes in the  
19 dynamics of their prey, as predator demographic parameters are tightly linked to variation  
20 in prey density (Tannerfeldt and Angerbjörn 1996). Currently, weakening population  
21 cycles of rodents are being increasingly reported in sub-arctic and boreal areas, where  
22 many predators of these rodents are in decline (Hörnfeldt et al. 2005, but see Brommer et  
23 al. 2010, for a case of population cycle coming back after disappearance). Nevertheless, in  
24 nomadic species, the relative effects on breeding parameters of habitat heterogeneity, food  
25 abundance and arrival time at the breeding grounds are poorly understood. Consequently,

1 understanding the factors determining spatial and temporal variation in breeder numbers  
2 and reproductive success is crucial to assessing the risks posed to specialists by global  
3 environmental change, and developing targeted conservation programmes for these species  
4 (McKinney and Lockwood 1999; Warren et al. 2001; Julliard et al. 2004).

5

6 Breeding habitat quality can influence reproductive and survival rates through variations in  
7 predation risk (Caro 2005), microclimatic conditions at the breeding site (Walsberg 1995)  
8 or food supply in nearby foraging habitats (Klopfer and Ganzhorn 1985; Hakkarainen et al.  
9 1997; Newton 2003). The dynamics of specialist nomadic predator populations are strongly  
10 affected by inter-annual changes in the availability and distribution of prey (Angerbjörn et  
11 al. 1999; Nielsen 1999), giving rise to variation in local breeding densities, primarily  
12 through immigration and emigration of breeding individuals in response to feeding  
13 conditions (Newton 2007). Furthermore, some nomadic specialist raptors are long-distance  
14 migrants, for which decisions made prior to and during migration from the wintering to the  
15 breeding grounds can have major effects on reproductive success and survival (Moller  
16 1994; Berthold 2001). Such effects may be mediated by factors such as condition upon  
17 arrival on the breeding grounds, or arrival date. In addition to their having to find areas of  
18 high prey abundance at the start of the breeding season, nomadic migrants are therefore also  
19 subject to additional costs and constraints associated with long migration.

20

21 The Pallid Harrier *Circus macrourus* is a specialist predator of voles (Terraube et al. 2011)  
22 and a long-distance migrant (birds breed in Russia and Central Asia, and winter in India or  
23 Africa; Ferguson-Lees and Christie 2001; Terraube et al. in press). To date, little is known  
24 about the relationship between voles and harrier breeding parameters (although see  
25 Terraube et al. 2011 for preliminary data). Nomadic behaviour in the Pallid Harrier has

1 been described through large changes in numbers between years at a local scale (Bragin  
2 2003), and more recently through satellite tracking (Terraube 2010; Terraube et al. in  
3 press). Substantial population decreases have been reported in many areas of the Pallid  
4 Harrier's breeding range, particularly in the peripheral populations breeding west of the  
5 Ural River (Davygora and Belik 1994; Bukreev 1997). Trends of the Asian core  
6 subpopulations have been less well documented, although local declines have been noted  
7 in several areas (Bragin 2003; Davygora and Belik 1994). As a result, the global  
8 conservation status of this species is now classified as 'Near Threatened' (Collar et al.  
9 1994). Population declines may be associated with breeding and wintering habitat  
10 degradation and reduced prey availability due to land-use changes, and/or high mortality  
11 rates during migration and on the wintering areas (Birdlife International 2003; Terraube  
12 2010). However, it has been recently suggested that its vulnerable conservation status may  
13 be linked to its specialist foraging strategy (Terraube et al. 2011). Therefore, getting to  
14 grips with the way in which factors such as prey abundance, habitat and time of year  
15 influence breeding numbers and performance could greatly improve our understanding of  
16 Pallid Harrier population dynamics and our ability to effectively set conservation priorities  
17 within the core breeding areas of this species.

18

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

1 timing of breeding (as a surrogate of the duration of the pre-breeding prospecting period)  
2 affect the breeding success of Pallid Harriers at a local scale.

3

## 4 **Methods**

5

### 6 *Study area*

7

8 We conducted fieldwork in the Naurzum National Nature Reserve and surrounding areas  
9 (hereafter referred as to “study area”) in north-central Kazakhstan (Fig. 1; Kostanay Oblast,  
10 51°N, 64°E) in June 2000, June 2006, May-July 2007 and 2008, and early June to mid-July  
11 2009. The study area, located at the southern limit of Siberian forests and northern limit of  
12 Eurasian steppes, is characterised by a mosaic of dry steppes, riverbeds, bushy areas and  
13 woodland patches (Katzner et al. 2003; Terraube 2010). We monitored an area of ca. 700  
14 km<sup>2</sup> (we estimated survey area by assuming a visibility of 1 km from the network of  
15 accessible tracks that we regularly travelled within the overall area, which totalled ca. 350  
16 km in length).

17

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

20

### 21 *Local prey abundance*

22

23 Small mammals such as voles exhibit strong inter-annual fluctuations in abundance in  
24 Kazakhstan (Bragin, 2003; Davies et al. 2004). We estimated vole abundance directly in  
25 the study area in 2006 (in June) and 2007-2009 (from late May to early July), using an

1 index based on the occurrence of fresh vole droppings. This index is correlated with  
2 estimates of vole abundance derived from trapping methods (Tapper 1979; Madders 2003).  
3 Twenty-five quadrats (25 x 25 cm) were randomly located in each of 11 (2006) and 24-25  
4 (2007, 2008 and 2009) plots (each plot being a ca. 500 m<sup>2</sup> area located within the study  
5 site). Each quadrat was sampled for the presence (1) or absence (0) of fresh (less than one  
6 week old) vole faeces (moist and greenish in colour). Presence/absence scores were then  
7 summed across the 25 quadrats in each plot, and averaged across sampled plots, to obtain  
8 an index of vole abundance (Madders 2003). We located the plots in the main vegetation  
9 types present in the study area (dry steppes, sandy steppes, rye-grass (*Lolium* sp.) or wet  
10 steppes, steppe along rivers, hereafter called riverine steppe and agricultural areas). The  
11 position of each quadrat differed between assessments and was determined by walking 20  
12 paces from the previous quadrat. In 2006, we did not sample rye-grass steppes. We did not  
13 quantify vole abundance in 2000, but we were able to estimate the vole abundance index  
14 from the relationships between our vole abundance index and the % of small mammals in  
15 the diet of Pallid Harriers (assessed through pellets collection and analysis, see Terraube et  
16 al. 2011 for further details) for the other four study years (vole index = 0.143 × [% small  
17 mammals] -2.03; R<sup>2</sup> = 0.958; see Terraube et al. 2011). This relationship gave an estimated  
18 vole abundance index of 8 for the year 2000 (Terraube et al. 2011).

19

#### 20 *Pallid Harrier abundance*

21

22 We located nests in the study area by following males carrying prey and locating where  
23 females landed after a food pass. During the first survey in 2000, we visited a total of 24  
24 Pallid Harrier nests (out of 35 located) and five more Pallid Harrier broods were found  
25 after fledging. In June 2006, we found 46 Pallid Harrier nests and visited 45. During 2007,



1 only 5 nests were located and 2 were visited; in 2008, we found and visited a total of 31  
2 nests and in 2009, 10 nests (out of 12 located) were visited. The location of all nests and  
3 known pairs was recorded using a GPS. Nest location was subsequently plotted in a GIS  
4 (ArcView 3.2, ESRI Inc. and Redlands, CA). In all cases, we estimated Pallid Harrier  
5 breeding abundance in the study area as number of located nests in relation to survey effort  
6 (calculated as number of man-days in each study year, see Table 1).

7

8 E. & A. Bragin conducted roadside counts to assess the relative abundance of all raptor  
9 species in the steppe habitats of north Kazakhstan. From this data set, we extracted the  
10 Pallid Harrier sightings. This included roadside counts carried out in the Naurzum region  
11 (in an area larger than, and including, the study area: labelled as zone 4 in Fig. 1) over a  
12 13-year period (1997-2009), as well as roadside counts in four other areas of steppe habitat  
13 in surrounding regions (labelled as zones 2, 3, 5 and 7-8 in Fig. 1) during a varying number  
14 of years, depending on survey areas (not all areas were surveyed for the whole time-period  
15 1997-2009). During surveys, both observers scanned for raptors, while driving at 30-  
16 40km/hr along road transects, between sunrise and sunset (08:00-20:00), with regular stops  
17 to accurately identify species using 10 x 42 binoculars. All counts were made during the  
18 breeding season (from May to middle July), and in good weather conditions, with good  
19 visibility and light winds. All individuals seen perched or flying, within view on either side  
20 of the roads, were counted. The length of transects (measured using the vehicle odometer  
21 and road maps), totalled 23 832 km. Pallid Harrier survey data are presented as the number  
22 of birds observed per 100 km of road transects in a given area (Fig. 1) and year.

23

24 *Estimation of Pallid Harrier breeding parameters*

25

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

6

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

18

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

25

1 During 2007-2009, all the nests we found were checked a minimum of three times to  
2 determine clutch size, brood size at three weeks and nesting success. In contrast, fieldwork  
3 in the first two years (2000 and 2006) covered only part of the breeding season and  
4 therefore the evaluation of breeding parameters was necessarily restricted and subject to  
5 some biases. For example, final clutch size was known for late breeders (which were still  
6 incubating eggs at the time of the first nest visit), but not for all early breeders (because  
7 some clutches had hatched before the first visit). In order to make sure that observed trends  
8 were not unduly influenced by such biases, we used only those nests for which the final  
9 clutch size was known. On the other hand, fledging success was not always known for late  
10 breeders (which had not fledged by the time of our last visit). When a nest had not been  
11 followed until fledging, we approximated fledged brood size as the brood size at last visit  
12 (if the last visit had occurred when the nestlings were at least > 15 days old). If the last visit  
13 had occurred with very small nestlings, we excluded that nest from this analysis. Thus,  
14 fledged brood size in these two years (2000 and 2006) may be overestimated. However,  
15 most of the nestling mortality in harriers occurs in the first two weeks after hatching  
16 (Castaño, 1995; Arroyo, 2002; Redpath et al. 2002), and nestling mortality is likely to be  
17 small particularly in high food abundance years (such as 2000 and 2006, Terraube et al.  
18 2009), so we believe this bias is likely to be small. Sample size varied among different  
19 models according to the information collected and available from each nest. We are aware  
20 that using different datasets to test different models could be a potential source of bias, but  
21 we preferred to do so in order to use all available information, as using only nests for  
22 which all information was available would strongly reduce sample size, and other types of  
23 biases may arise.

24

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

3

#### 4 *Statistical analyses*

5

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

12

13 To analyse our time-series of Pallid Harrier abundance, we used the PAST software  
14 (Hammer and Harper 2005) and performed a spectral analysis to search for periodicity in  
15 the abundance fluctuations.

16

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

22

23 To identify the factors linked with variations in breeding success in our study population,  
24 we also used GLMs. Clutch size and fledged brood size were modelled using a log-link  
25 function with Poisson errors, while hatching and nesting success were modelled as

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

16

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

19

## 20 **Results**

21

### 22 *Vole and Pallid Harrier abundance*

23

24 Vole abundance in the study area varied greatly between study years, ranging from 0 to 8.8  
25 (Table 1). Variation in vole abundance was significantly explained by year ( $\chi^2_3 = 283.34$ ; P

1 < 0.0001), habitat ( $\chi^2_4 = 154.59$ ;  $P < 0.0001$ ), and their interaction ( $\chi^2_{11} = 61.80$ ;  $P <$   
2 0.0001). In 2006 and 2008, when voles had respectively high and intermediate abundance,  
3 vole indices were present in almost all habitat types, although highest abundances were in  
4 tall and dense herbaceous vegetation along the rivers, where voles also concentrated in  
5 lower abundance years (Table 2). In 2008 only, highest vole abundances were found in rye-  
6 grass steppes.

7

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

12

13 Pallid Harrier relative abundance estimated from road-censuses in the Naurzum region  
14 showed strong interannual variations during the 13-year period of the survey (Fig. 3). A  
15 spectral analysis conducted on these data show a peak frequency at 0.173, which would be  
16 indicative of a c. 6-year period. Although the power at this peak frequency did not reach  
17 statistical significance ( $0.05 < P < 0.10$ ), our short-time series is consistent with a 6 year-  
18 period cycle in Pallid Harrier abundance. Within our study period, there were two marked  
19 peaks in harrier abundance (2000 and 2006), and three years of very low harrier density  
20 (1998; 2003 and 2009, Fig. 3).

21

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

25

1 *Factors driving Pallid Harrier breeding success*

2

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

5

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

9

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

13

14 Fledged brood size varied in relation to vole abundance and habitat type, and also in  
15 relation to their interaction, but no effect of breeding timing was found once controlling for  
16 the other variables (Table 3). Fledged brood size increased with increasing vole abundance,  
17 but both the intercept and the slope of this relationship varied among habitats (as evidenced  
18 by the interaction between vole abundance and habitat, Table 3). Overall, fledged brood  
19 size was higher in rivers and lakes when voles were abundant, but was higher in steppes  
20 when they were scarce.

21

22 **Discussion**

23

24 We found that in Pallid Harriers: i) local breeding numbers show a strong numerical  
25 response to vole density; ii) regional abundance greatly varied among years, possibly with

1 a 6-year period, and apparently asynchronously among contiguous regions and iii) breeding  
2 success depends on vole abundance, and also on timing of breeding and breeding habitat  
3 type: late nesters laid smaller clutches and had higher probabilities of failing, particularly if  
4 nesting in riverine habitats (which are used more frequently as the season progresses).  
5 Below we discuss these findings and their implications for our understanding of the  
6 ecology and conservation needs of nomadic predator specialists.

7

8 *Numerical response of Pallid Harrier to vole abundance variations.*

9

10 The strong numerical response observed at the local scale, in addition to the changing  
11 patterns of relative abundance of Pallid Harriers at the regional scale, are consistent with  
12 high mobility and a nomadic breeding strategy (Ferguson-Lees and Christie 2001;  
13 Terraube et al. 2011). Data from satellite tracking has confirmed both of these traits in  
14 Pallid Harriers showing that they undertake prospecting trips up to 3000 km between  
15 returning from their wintering areas and settling on their breeding grounds, lasting up to  
16 three weeks (Terraube 2010) and have very large breeding dispersal distances (mean  $652 \pm$   
17  $271$  kms; Terraube 2010 and unpublished data). This suggests that, during the breeding  
18 period, Pallid Harrier is a true nomadic, rodent-specialist raptor. The large-scale variations  
19 in breeding density we found could be due to inter-annual movements of Pallid Harriers  
20 between different breeding areas in response to large-scale fluctuations in vole densities.

21

22 The numerical response observed between breeding harriers and voles (Fig. 2) suggests  
23 that Pallid Harrier abundance is tightly correlated with vole abundance at the local scale  
24 (see Sundell et al. 2004, for similar assumptions about rodent-specialist raptors in northern  
25 ecosystems). Assuming this is the case, the cyclical pattern in breeding Pallid Harrier



1 numbers, suggested by our relatively short time series, raises the possibility of a similar  
2 cycle in vole populations, with a 6 year period (Fig. 3) and little synchrony between  
3 neighbouring regions (Fig. 4). This should be confirmed with longer time-series of vole  
4 abundance (a 13-year time series is too short for confirming a 6-year period cycle as it can  
5 only include two peaks or lows), also looking at larger scales. Studies on microtine  
6 dynamics in Scandinavia and western Europe at similar latitudes have shown clear 3-4  
7 years cycles (Korpimaki and Norrdhal. 1991; Salamolard et al. 2000; Gilg et al. 2006;  
8 Lambin et al. 2006) and greater spatial synchrony of vole fluctuations (Spitz 1977;  
9 Bowman et al. 2000; Huitu et al. 2005), also reflected in the patterns of variation in the  
10 abundance of vole specialist raptors and other predators in those areas.

11

12 The patterns of rodent density variations observed in the study area might result from the  
13 interaction of several mechanisms. Two climatic parameters, namely the amount of rainfall  
14 and temperature are known to affect reproduction and survival of small rodents (Koontz et  
15 al. 2001). Additionally, climatic variables may interact with density dependent processes,  
16 as the interaction between density and mean temperatures has been shown to strongly  
17 influence vole survival (Goswami et al. 2011). At a more local scale, grazing intensity has  
18 been also shown to influence vole densities in central-asian steppes (Zhang et al. 2003).  
19 Finally, predation has an important role in shaping vole population dynamics and often can  
20 limit the population growth of voles (Sundell, 2006). Steppes of north-Kazakhstan harbour  
21 a highly diverse predator guild preying potentially on small mammal species, including  
22 specialist (Pallid Harriers, Short-eared Owls *Asio flammeus*) and generalist predators (two  
23 fox species, mustelids and a diverse raptor community). Therefore, the role of predation  
24 interacting with the previous cited mechanisms cannot be excluded in explaining the  
25 variation in rodent densities observed.

1

2 *Factors linked with variations in Pallid Harrier breeding parameters.*

3

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

15

16 Interestingly, breeding habitat type also influenced nest failure and fledged brood size,  
17 after taking into account vole abundance. The influence of habitat on reproductive output  
18 could be driven by i) inter-habitat variation in prey abundance or availability; ii) vegetation  
19 structure (height or density) around the nest influencing local micro-climate conditions;  
20 and iii) inter-habitat differences in predation risk. Of the five habitats sampled for voles,  
21 riverine steppes held the highest densities of voles (Table 2). We might therefore expect  
22 this habitat to be selected by nesting Pallid Harriers, because of the advantages to central-  
23 place foragers of nesting near areas with high prey density (Orians and Pearson 1979). The  
24 large size of broods fledged from this habitat when voles were abundant also implies that  
25 riverine steppe is high quality with regard to food supply. However, breeding failure was

1 highest in nests located in riverine habitats or in steppe vegetation near rivers, possibly as a  
2 result of higher predation rates by mammalian predators such as foxes and mustelids,  
3 particularly during incubation (Terraube et al. 2009). This result should however be taken  
4 with caution because of a possible bias in the nest stage discovery of nests in this habitat  
5 (Table 4), as a higher proportion of nests were discovered in this habitat during incubation,  
6 therefore potentially over-estimating nesting success in other habitats if nests failed during  
7 incubation were unnoticed. Given their corridor-like nature in otherwise homogeneous  
8 steppe habitats, the riverine habitats may be used as regular foraging routes by terrestrial  
9 predators, potentially resulting in a higher predation rate (Terraube et al. 2009). In contrast,  
10 in lakes, nests might be less accessible for terrestrial predators.

11

12 Nesting habitat preferences also varied over the course of the breeding season, with early  
13 breeders using all habitats while late breeders favoured riparian areas. In addition, breeding  
14 habitat preference varies throughout the season, as early breeders used all habitats whereas  
15 late breeders favoured riverine habitats for nesting (Terraube et al. 2009). Microclimate at  
16 the nest site can explain differences in breeding success through the influence of  
17 temperature on hatching success and chick survival (Öst et al. 2008). Climate in Central  
18 Asia is strongly continental with very low winter temperatures (between -20/-40°C) and  
19 short, very hot summers (up to 40°C). Very high temperatures are particularly frequent in  
20 the study area during the month of June (authors pers. obs; <http://www.worldclimate.com>),  
21 corresponding to the laying period of late-breeding Pallid Harriers. This could lead these  
22 birds to favour shaded nest sites in riverside reedbeds, which are among the only areas  
23 providing such protection from the sun in steppe landscapes. This could explain the strong  
24 selection of riverine habitat in our study area by late breeders, despite the association of  
25 this habitat with high nest predation rates. Reeds growing in riverbeds are the only habitat

1 providing this type of protection and could explain the strong selection of this habitat in  
2 our study area in late breeders, maybe in a counter-selective pattern as these habitats are  
3 associated with higher predation risk (Terraube et al., 2009).

4

5 Finally, timing of breeding also influenced breeding output, due to an effect on clutch size  
6 and hatching success (mainly through higher predation rates in the breeding habitats  
7 selected late in the season). While the effect of the timing of breeding on clutch size is *a*  
8 *priori* unlikely to be affected by the stage at which nests were found, the same might not  
9 be true for hatching success. Because we found fewer early nests than late nests during  
10 incubation (Table 4), we may have missed some failed early nests, and thereby over-  
11 estimated hatching success in early breeders. Hence, the relative differences in terms of  
12 hatching success should be taken with caution. A seasonal decrease in clutch size and  
13 overall reproductive success has been reported in numerous bird species and has been  
14 associated with higher parental quality of early-breeding birds, and decreased in  
15 environmental quality through the breeding season, or both (Arnold et al. 2004). However,  
16 in the case of Pallid Harriers the onset of laying occurs over more than two months, and the  
17 distribution of lay dates throughout the season is bimodal, suggesting that there may be  
18 multiple factors influencing timing of breeding (Terraube et al. 2009). Additionally, the  
19 lack of an obvious negative relationship between lay date and either brood size or nest  
20 success suggests that variation in breeding output between both groups is not exclusively  
21 due to variation in individual quality.

22

23 We propose that the observed pattern could be a consequence of intrapopulation  
24 differences in pre-breeding prospecting strategy. A positive relationship between breeding  
25 dispersal distance and the reproductive costs of dispersal (sometimes influenced by the

1 breeding individual's quality) has been shown by several studies (Danchin and Cam 2002;  
2 Cam et al. 2004; but see Doligez and Part 2008). Pallid Harriers undertake large breeding  
3 dispersal movements, associated with a long prospecting period after birds arrive from  
4 their wintering areas (Terraube 2010). Birds returning to Kazakhstan, prospect for  $21 \pm 15$   
5 days, and travel  $1720 \pm 753$  km during this time ( $n = 3$  females and 4 reproductive events;  
6 unpublished data). This inter-individual variation in prospection duration and distance  
7 travelled suggests that some individuals might be better than others at quickly locating high  
8 vole abundance areas for breeding. A possible explanation for the decrease in clutch size  
9 among late breeders is that long prospection period incurs a fitness cost in terms of body  
10 condition due to the distance travelled.

11

## 12 **Conclusions**

13

14 Breeding success of Pallid Harriers depends primarily on several parameters; vole  
15 abundance (the preferred prey), but also on local habitat heterogeneity and on timing of  
16 breeding. The latter is likely to be the consequence of how long it takes individuals to find  
17 good breeding areas, with a potential cost of long prospection periods (Newton 2003;  
18 2007).

19

20 Second, our data suggest that vole abundance in Kazakhstan fluctuates cyclically, possibly  
21 with a 6-year period, but asynchronously at a large spatial scale. Such a long period and  
22 pattern of variation may make it potentially difficult for harriers to accurately predict when  
23 and where the next vole outbreaks will occur. A lack of synchronicity at the regional scale  
24 implies that it should be possible for a returning harrier to find good breeding areas within a  
25 few hundred kilometres of a previous breeding place that happens to have no voles upon

1 arrival from the wintering grounds. However, if vole dynamics change, the efficiency of  
2 this strategy might also change.

3

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

8

9 Climate change in central Asia is expected to increase rainfall stochasticity and increase  
10 summer heat in the southernmost areas (Lioubimtseva and Henebry 2009), with warmer  
11 and wetter conditions at the northern latitudes (Yu et al. 2003). This would increase  
12 rangeland productivity and as a consequence cattle numbers, and allow further agricultural  
13 intensification across the northernmost areas (Joyner et al. 2010; and see Baker et al. 1993  
14 for a study conducted at similar latitudes to Kazakhstan). Changes in grazing and  
15 agricultural patterns in the northern part of the Pallid Harrier's breeding range in  
16 conjunction with increasing aridity in the southern areas would have a strong impact on the  
17 steppe vegetation and are likely to have impact on the structure of steppe vegetation and,  
18 consequently, on vole dynamics. Agriculture intensification is also known to reduce small  
19 rodent densities (Butet and Leroux 2001; Jacob, 2003; Aschmanden et al. 2007) and  
20 Kazakhstan has experienced a strong economic increase in recent years, associated with  
21 agricultural intensification and a net recent growth in livestock numbers after years of  
22 decrease (Bragin 2003). Climate and land-use changes could act simultaneously on the  
23 vegetation structure and composition of central Asian steppes through a general process of  
24 pasture degradation. This could increase the number of sites showing simultaneously low  
25 vole densities, implying that Pallid Harriers would need longer prospecting phases to find

1 good breeding areas, with associated reductions in breeding success, which could  
2 negatively influence the long-term viability of the core Kazakh and Siberian Pallid Harrier  
3 populations.

4

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

10

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12

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22

23

24

25

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2

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26

1 Table 1. Vole abundance indices and reproductive parameters of Pallid Harriers during the  
 2 five-year study in the Naurzum region (north-central Kazakhstan). Sample sizes (in  
 3 brackets) refer to number of nests. Data are given as means  $\pm$  SD.

Year	2000	2006	2007	2008	2009
Vole index	[8.0]*	8.8 $\pm$ 8.1 (11)	0 $\pm$ 0 (25)	4.0 $\pm$ 5.1 (24)	1.2 $\pm$ 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**	0.77	0.81	0.05	0.33	0.15
Mean laying date (Julian days) (range; sample size)	31.3 $\pm$ 18.9 (10-71; 24)	38.3 $\pm$ 16.8 (11-64; 40)	42.9 $\pm$ 15.3 (25-59; 7)	35.4 $\pm$ 12.7 (7-55; 31)	50.4 $\pm$ 8.4 (35-60; 9)
Clutch size	5.7 $\pm$ 0.8 (12)	5.6 $\pm$ 1.3 (26)	4.0 $\pm$ 0.0 (2)	4.8 $\pm$ 0.7 (24)	3.5 $\pm$ 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 $\pm$ 1.7 (16)	3.2 $\pm$ 1.6 (10)	na	2.6 $\pm$ 1.3 (22)	2.0 $\pm$ 0 (1)

5  
 6  
 7 \* *Estimated data, see methods*

8 \*\*Number of breeding pairs found/survey effort

9

1 Table 2. Vole abundance estimates in relation to habitat. Sample sizes (in brackets) refer to  
 2 number of plots. Data are given as means  $\pm$  SD.

3

	2006	2007	2008	2009 4
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) 6
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)



Table 3. Results of the final GLM models showing the variables that influence variations in the breeding parameters of Pallid Harriers. Estimates are given as means  $\pm$  SE.

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

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

Figure 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).

Figure 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). When also including this estimation for 2000, the relationship between vole abundance and observed Pallid Harrier density was as follows:  $[\text{Pallid harrier density}] = (0.0859 \times [\text{vole index}]) + 0.0269$ .

Figure 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).

Figure 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 were 2, 3, 4, 5 and 7-8 in Figure 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.

Fig. 1.

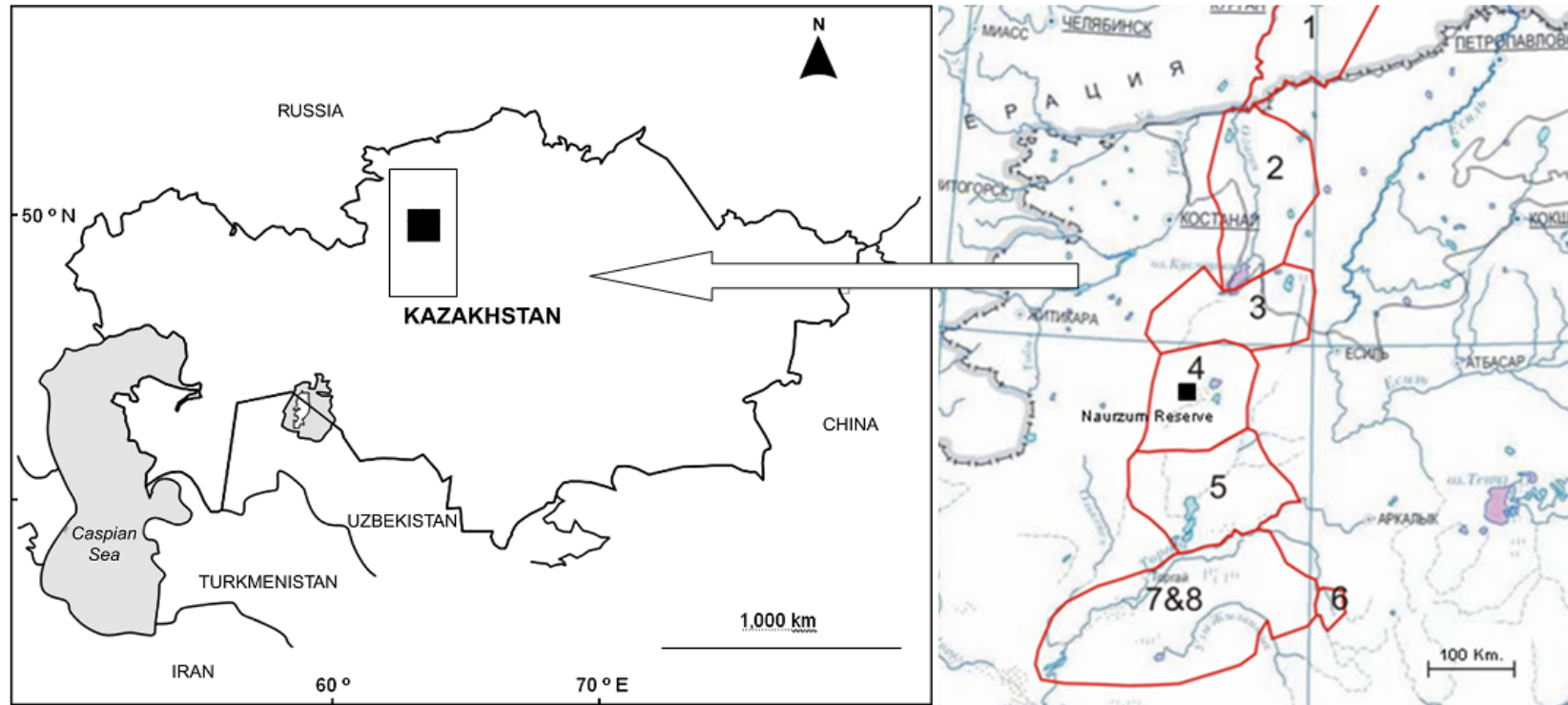


Fig. 2

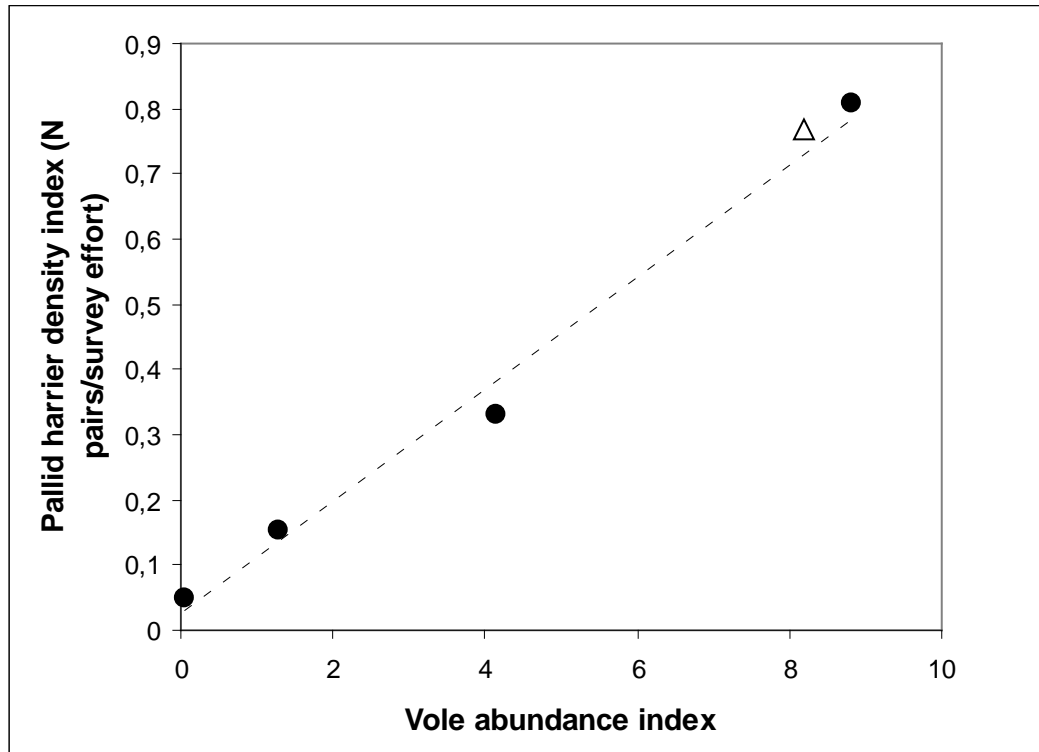


Fig. 3

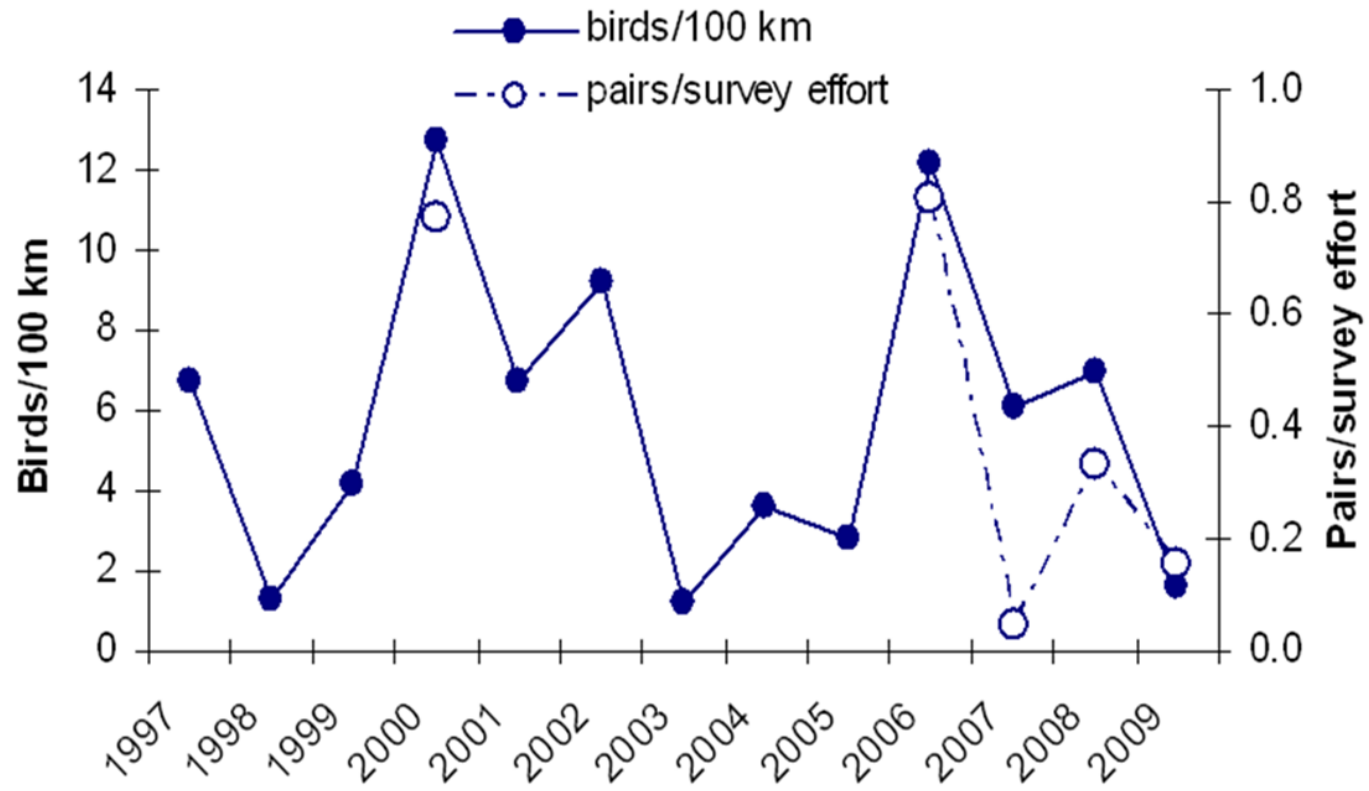


Fig. 4.

