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Condition, reproduction and survival of barn swallows from Chernobyl

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Summary

1. We investigated the relationship between radiation arising from the fall-out due to the explosion of the nuclear reactor at Chernobyl, Ukraine, and body condition, rate of reproduction and survival in a migratory passerine bird, the barn swallow *Hirundo rustica* L., by comparing a contaminated region and a control region (Kanev) during 6 years between 1991 and 2004.
2. The fraction of nonreproducing adults was on average 23% in Chernobyl compared with close to zero in Kanev and other European populations.
3. Body condition as estimated from body mass was similar in Chernobyl and Kanev. Although laying date did not differ significantly between the two regions, clutch was reduced by 7%, brood size by 14% and hatching success by 5% in the Chernobyl region relative to the control area.
4. Annual adult survival, estimated from mark–recapture analyses, was on average 28% in the Chernobyl region, but 40% in Kanev.
5. The relationships were generally confirmed in rank correlation analyses between response variables and ambient radiation levels in different colonies.
6. The overall findings are consistent with the hypothesis that radioactive contamination in the Chernobyl region has significant negative impact on rates of reproduction and survival of the barn swallow. We hypothesize that these effects are mediated by antioxidants and/or mutations.

Key-words: antioxidants, body condition, clutch size, hatching success, *Hirundo rustica*, nonbreeding, population change, survival.

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Introduction

Natural levels of radioactivity vary considerably, and even naturally high levels may have biological consequences. For example, approximately 17 000 people die from radon-induced lung cancer in the USA each year (Lubin & Boice 1997). The extent to which natural levels of radiation affect wild animals and plants is almost entirely unknown. Contamination arising from nuclear weapons tests or accidents such as those at Three-mile Island and Chernobyl has affected vast areas. In the case of Chernobyl more than 5000 km^2 have been contaminated in Ukraine and Belarus to the extent that these areas have been completely depopulated (Anonymous 1996). Immediately following the explosion at the Chernobyl reactor, the main source of radiation were I^{131}, Cs^{137} and Sr^{90} (Shestopalov 1996). Owing to its short half-life (8 days), I^{131} is no longer a significant concern. However,

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Cs^{137} and Sr^{90} are both strong β-radiation emitters with half-lives on the order of 30 years (Shestopalov 1996), and will thus be present in significant amounts for many hundred years to come. Vast areas outside the exclusion zone are affected by lower levels of radiation that greatly exceed natural background levels and such contamination may have consequences for survival and reproduction of humans and other organisms. For example, it has been shown that survival rates of humans and animals can be reduced in contaminated areas (Robbins & Adams 1989; Kerber *et al*. 1993; Ellegren *et al*. 1997; Jacob *et al*. 1998; Akleyev *et al*. 2002; Semjuk *et al*. 2002). Effects of low-level radiation on reproductive success of free-living organisms have only been examined to a very small extent (e.g. Fair & Myers 2002). Such effects of radiation on life history may have consequences at the population level due to reductions in population size (Zakharov & Krysanov 1996; Ellegren *et al*. 1997). Given the size of the contaminated areas from the Chernobyl accident any genetic or physiological effects will affect very large populations of plants and animals, potentially with consequences well beyond the directly affected areas due to migration. These findings from Chernobyl contrast with the conclusions from the Hiroshima and Nagasaki studies, which found no long-term effects on reproduction or mutation (e.g. Awa *et al*. 1987; Neel *et al*. 1988). However, the amounts and the isotopes involved differed dramatically, potentially accounting for these differences.

The mechanisms resulting in reduced survivorship and fecundity in populations living in contaminated areas may be elevated mutation rates or physiological processes being affected by a reduction in levels of antioxidants. Genetic studies have reported increased mutation rates in humans and barn swallows *Hirundo rustica* L. from the radioactive contaminated area around Chernobyl in Ukraine (Dubrova *et al*. 1996; Ellegren *et al*. 1997; Weinberg *et al*. 2001), and such mutations may negatively affect a range of phenotypic traits (Møller & Mousseau 2001, 2003). Second, antioxidants may be depleted in contaminated areas (Chaialo, Bereza & Chobot'ko 1991; Bazhan 1998; Ben-Amotz *et al*. 1998; Ivaniota, Dubchak & Tyshchenko 1998; Neyfakh, Alimbekova & Ivanenko 1998a,b; Lykholat & Chernaya 1999; Kumerova *et al*. 2000; Møller, Mousseau & Surai 2005) and such reductions may reduce clutch size (Blount *et al*. 2003) and affect other life-history traits.

The aims of this study of the barn swallow were to quantify: (1) the frequency of reproduction; (2) reproductive rates; and (3) survival rates in the radioactively contaminated region around Chernobyl, Ukraine, and in a control region around Kanev more than 250 km to the SE of the main contaminated area around Chernobyl. We further investigated these relationships by determining the association between our response variables and local levels of radiation measured in the field at each bird colony.

Materials and methods

STUDY SPECIES

The barn swallow is a *c*. 20-g aerial insectivorous passerine bird with long-distance migration (Møller 1994). Populations in Europe winter south of the Sahara, and adults have extremely low levels of storage and circulating antioxidants upon arrival to the breeding grounds (Ninni *et al*. 2004). Males arrive before females and attract females by aerial displays of their red throat patches, long tails and elaborate song (Møller 1994). Once a male is mated, the pair will build a nest, where the female will lay eggs and incubate. Females deposit significant amounts of carotenoids and other antioxidants in eggs, resulting in a second minimum in circulating antioxidants in females during the laying period (Saino *et al*. 2002). Both males and females feed nestlings and often raise a second brood before returning to Africa in September–October (Møller 1994).

Male barn swallows in Chernobyl have dramatically increased asymmetry in their elongated outermost tail feathers and much paler throat coloration compared with males from a control area and with males predating the Chernobyl accident (Møller 1993). Long-tailed males in particular are very pale compared with controls (Camplani, Saino & Møller 1999). These findings suggest that antioxidant availability is reduced in radioactively contaminated areas around Chernobyl.

STUDY AREAS

We studied barn swallows in parts of the southern and western sector just outside the exclusion zone of the Chernobyl area (Shestopalov 1996). We visited villages and stopped to check collective farms for the presence of barn swallows. We drove along all public roads to visit villages and collective farms in areas with high levels of radiation outside the exclusion zone near Chernobyl. We visited all such areas south of the exclusion zone. While visits to areas with high levels of radiation is nonrandom, we see no reason why such a selection should be associated with farming practice, soil quality or abundance of insects, which are the main food for barn swallows. If barn swallows were recorded, we attempted to capture as many adults as possible at windows and doors of farm buildings using mist nets. The villages visited and used for the study included Guda-Katyuzhanka, Kathyuskanka, Obukovichy, Phenevichy, Ivankov, Vakhovka, Glybovka, Pribirsk, Dytiatku, Pysky, Martynovichi, Bober, Vesniane and Dymir (Fig. 1). As a control area we used Kanev *c*. 220 km south-west of Kiev that has a relatively low level of contamination. The relatively low level of contamination was confirmed by our own measurements of radioactivity. The control villages visited and used for the study included Kanev, Stepatsy and Stepanetske (Fig. 1). In the control area around Kanev we

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Fig. 1. Location of study sites and levels of radiation in the Chernobyl and Kanev regions. Shaded areas represent areas where > 3 Curie of Cs^{137} per km^2 were deposited in 1986 (CIA 1996). The average radiation levels for sample sites located in the contaminated areas were 0·390 mR h^{-1} (SE = 0·317) at 14 breeding sites in the Chernobyl region. In the control region near Kanev (*c.* 150 km SSE of Chernobyl) radiation levels were on average an order of magnitude lower [0·025 mR h^{-1} (SE = 0·002)]. Approximate locations of field sites are indicated either as red stars (in contaminated areas) or green stars (relatively uncontaminated control areas).

similarly visited all the nearest villages to check for the presence of barn swallows on collective farms.

Several villages with barn swallows in the 1990s held no or only very few barn swallows during the last two visits, and these sites were therefore not included during these later visits. Sites were selected based on the number of barn swallows present, and farms where no or few barn swallows were left were omitted during later visits. Barn swallows commonly abandon breeding sites, and such abandonment is frequently associated with changes in farming practice (Møller & Mousseau 2001).

STUDY PERIODS

We worked in the two study areas during 10–29 June 1991 (APM), 16–24 June 1996 (APM), 6–12 June 2000 (APM, TAM), 4–11 June 2002 (APM, TAM), 7–13 June 2003 (APM, TAM) and 23–28 June 2004 (APM, TAM).

FIELD ESTIMATES OF RADIATION

We obtained radiation estimates from two sources; our own field measurements or measurements by the Ukrainian Ministry of Emergencies. We measured α, β and γ radiation levels at ground level directly in the field using a hand-held dosimeter (Model: Inspector, SE International, Inc., Summertown, TN, USA). We measured levels several (two to 10) times at each site and averaged the measurements. Our data were validated with correlation against data from the governmental measurements published by Shestopalov (1996), estimated as the mid-point of the ranges published. This analysis revealed a very strong positive relationship [linear regression on log-log transformed data: $F = 159{\cdot}46$, d.f. = 1,18, $r^2 = 0{\cdot}89$, $P < 0{\cdot}0001$, slope (SE) = 1·28 (0·10)], suggesting that our field estimates of radiation provided the same ranking of levels of radiation among sites as did published estimates. Similarly, the measurements by the Ministry of Emergencies were obtained by repeated standardized measurement of radiation at the ground level in a large number of different localities in Ukraine.

CAPTURE OF ADULT BARN SWALLOWS

We captured barn swallows by placing mist nets across open doors and windows in farm building. This method is highly efficient during the main breeding season, and we were able to catch more than 75% of all adults, according to estimates of capture probability based on the proportion of unbanded birds (see following section).

SIZE OF REPRODUCING POPULATION

We estimated the size of the breeding population at different farms by inspecting all nests and investigating these for signs of reproduction. As we conducted fieldwork at a time when all reproducing individuals would have started building nests (in Denmark 1000 km further north, no first clutch nests were initiated after 10 June during the study of more than 5000 clutches in 1970–2002, A. P. Møller, unpublished data), and a study of barn swallows in nearby eastern Hungary during 4 years also revealed that all first clutch nests were initiated by early June (P. Pap & A. P. Møller, unpublished data). All nests that were under construction, or contained fresh eggs or nestlings, were considered to represent cases of current year reproduction. We estimated the number of adult birds by means of mark–recapture analyses. When we had captured and banded adults for several hours, we recorded during the last hour of capture the number of banded and unbanded birds. We estimated the size of the total population as the total number of banded birds divided by the proportion of birds captured that were already banded during the last hour.

In an independent estimate of local population size we marked the white breast feathers of banded adult barn swallows with a permanent red marker pen. During the last hour before capture was terminated we counted the maximum number of adult barn swallows with and without red colour markings, using a pair of Zeiss 10 × 30 binoculars. Population size was in this case estimated as the total number of banded birds divided by the proportion of birds that were marked with the red pen. In small breeding colonies with a maximum of 10 breeding pairs we counted the maximum number of adult birds seen as almost all foraging usually takes place within a distance of 200 m from the breeding site, with occasional observations at distances of up to 500 m (Møller 1987; Ambrosini *et al.* 2002).

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We used the total number of birds divided by two as an estimate of total breeding population size.

In 2004 we checked all females carefully for a fully developed brood patch that is completely naked with no presence of feathers. Any adult female with feathers on the brood patch was considered to be a nonbreeder.

The size of the nonbreeding population and hence the number of nonbreeding females was the estimate of total adult population size minus twice the number of active nests.

BODY CONDITION OF ADULTS

Body condition reflects the amount of stored resources relative to the size of an individual, and body mass after controlling statistically for body size thus provides an unbiased estimate of such storage. We took 10 measurements of different morphological characters and weighed each adult barn swallow upon capture to the nearest 0·1 g with a Pesola spring balance. The correlation between body mass and structural body size measured as keel length was weak and not statistically significant (linear regression: $F = 1{\cdot}86$, d.f. = 1,629, $r^2 = 0{\cdot}001$, $P = 0{\cdot}17$). Hence, we used body mass in the subsequent analyses as a measure of body condition, as body mass was not confounded by body size. Body mass is highly repeatable among captures (Møller 1994).

REPRODUCTION

We visited all buildings at farms within the two study regions. Each was inspected for nests in use and all new nests (as evidenced from the absence of spider webs in the nest cup) were checked for content. Laying date was calculated for all nests with laying in progress (one, two or three eggs) assuming that one egg is laid per day. Similarly, for nests with nestlings we used size relative to a standard growth curve to estimate age in days and then back-calculated assuming an incubation period of 14 days (Møller 1994) and one egg being laid each day. Clutch size was estimated as the total number of eggs in nests with at least three eggs. Brood size was estimated as the number of nestlings that were at least 2 days old, thereby avoiding underestimates due to eggs that had not yet hatched. Unhatched eggs remain undamaged in nests, and hatching success was calculated as brood size divided by clutch size.

SURVIVAL ANALYSES

Survival analysis was based on data of 152 males and 151 females captured and recaptured in the Chernobyl region and 103 males and 98 females captured and recaptured at the Kanev region between 2000 and 2004. We estimated annual survival rates using capture–mark–recapture methods (Lebreton *et al.* 1992). The goodness-of-fit of the general Cormack–Jolly–Seber model (Clobert & Lebreton 1987) to the data was calculated using the program RELEASE (Burnham *et al.* 1987), and the bootstrap function of the program MARK (White & Burnham 1999). Modelling and estimation of survival and recapture rates was made with MARK (White & Burnham 1999). We considered the overdispersion value (c-hat) during model selection (Lebreton *et al.* 1992). Model selection among the studied models was based on the Akaike's Information Criterion by selecting the model with the lowest AICc value (Anderson, Burnham & White 1994) and Akaike weight (Anderson & Burnham 1999), and hierarchical likelihood ratio tests (LRT) were made by comparing a model with those nested within the model (Lebreton *et al.* 1992).

STATISTICAL ANALYSES

We used two types of analyses to test for associations between high levels of radiation and response variables. In the first series of analyses we used one-way analysis of variance to test for a difference between the Chernobyl and the Kanev region, using region as a fixed effect. In a second series of analyses we investigated the relationship between mean value for the response variable and measured level of radiation for each site.

Sample sizes differ among analyses because all variables could not be quantified for all nests.

We used parametric or nonparametric analyses depending on whether the distribution of variables deviated significantly from normal distributions. The proportion of nonbreeders and hatching success were square-root-arcsine-transformed and colony size and radiation level estimates were log-transformed before statistical analyses.

All values reported are means (± SE).

Results

FRACTION OF POPULATION REPRODUCING

We estimated the number of active nests and the number of adults present at a number of different sites (Table 1). The estimation of population size based on captures of individuals will only be reliable if captured individuals do not become trap shy. We tested for this effect by determining whether estimates based on captures differed from estimates based on sightings of birds that were dyed on their breast feathers after capture. Estimates based on different methods were highly consistent, with almost all variance occurring among sites rather than between methods (Table 1, $F = 640{\cdot}24$, d.f. = 11,12, $P < 0{\cdot}0001$). In 2004 we checked all females for the presence of a brood patch, and this method gave very similar results to estimates based on dyed birds ($F = 102{\cdot}40$, d.f. = 3,4, $P < 0{\cdot}0001$). There was considerable variation in the proportion of nonbreeding pairs, ranging from 0 to 67% across sites (Table 1). The frequency of nonbreeding pairs in the Kanev region was significantly lower than in the Chernobyl region

Table 1. Estimates of number of active nests and number of adult barn swallows in Chernobyl and Kanev regions 1996–2004

Site	No. active nests	No. birds from recaptures	No. birds from sightings of dyed birds	No. of birds counted	Nonbreeding birds (%)
1996					
Glybovka	7			16	12·5
Guda-Katyushanka	5			11	9·1
Ivankov	1			2	0·0
Obukhovchi	3			7	14·3
Phenevichy	2			4	0·0
Rudya-Dymerskaya	5			12	16·7
Kanev Reserve	7			14	0·0
Stepanetske	10			22	9·1
Stepantsy	10			21	4·8
Kanev Chicken Farm	10			20	0·0
2000					
Bobor	3			14	57·1
Pribirsk	15	34			11·8
Vesniane	5			18	44·4
Kanev	45	90	90		0·0
2002					
Bobor	1			6	66·7
Dytiatku	18	38			5·3
Pisky	36	100	102		28·7
Pribirsk	4	8		8	0·0
Vesniane	19	55	62		35·0
Kanev	45	90	90		0·0
2003					
Dytiatku	23	56	56		21·7
Pisky	26	54	55		3·9
Vesniane	8	12	12		50·0
Kanev	35	70	70		0·0
2004					
Dytiatku	25	59	60		18·0
Pisky	30	69	69		15·0
Vesniane	9	26	26		45·0
Kanev	15	30	30		0·0

(Fig. 2a; Mann–Whitney U-test, $z = 3{\cdot}18$, $P = 0{\cdot}002$). However, the frequency of 1·7% (SE = 1·2) in Kanev did not differ significantly from the value of 0% recorded in western Europe (one-sample t-test, $t = 1{\cdot}42$, d.f. = 26, $P = 0{\cdot}37$). There was a significant positive relationship between the frequency of nonbreeding pairs and local levels of radiation [Fig. 3; linear regression: $F = 35{\cdot}07$, d.f. = 1,26, $r^2 = 0{\cdot}57$, $P < 0{\cdot}0001$, slope (SE) = 0·31 (0·05)].

Previous studies have shown that nonbreeding males aggregate in large colonies, while nonbreeding females have never previously been recorded (Møller 1988). There is usually a small excess of males among adult barn swallows (9·4%; SE = 1·0) in Denmark (Møller 1994; A. P. Møller, unpublished data). This was also the case in Ukraine with 52·85% of 932 adults captured being males. Colony size could have confounded the relationship between frequency of nonbreeders and level of radiation. However, colony size was not related to levels of radiation (linear regression based on log-transformed data: $F = 0{\cdot}12$, d.f. = 1,26, $r^2 = 0{\cdot}00$, $P = 0{\cdot}73$). Also, the relationship between the frequency of nonbreeding pairs and local levels of radiation was not confounded by colony size measured as the total number of adult birds present [multiple linear regression: $F = 16{\cdot}87$, d.f. = 2,25, $r^2 = 0{\cdot}57$, $P < 0{\cdot}0001$, slope (SE) for radiation = 0·31 (0·05), $t = 5{\cdot}79$, $P < 0{\cdot}0001$; slope (SE) for log-transformed colony size = –0·01 (0·10), $t = 0{\cdot}12$, $P = 0{\cdot}91$].

The sex ratio among adults was 53·42% ($n = 556$) in Chernobyl and 52·13% ($n = 376$) in Kanev, with no significant difference between areas ($G = 2{\cdot}76$, d.f. = 1, $P = 0{\cdot}10$). Thus, there were no clear differences in sex ratio among areas in Ukraine.

BODY CONDITION OF ADULTS

Adult barn swallows differed in body mass in relation to level of contamination. Barn swallows from the Chernobyl region were slightly lighter than conspecifics from the Kanev region (Fig. 2b). There was a sex difference in body mass, but this effect was similar in the two regions as evidenced by a nonsignificant interaction term between sex and region ($F = 0{\cdot}42$, d.f. = 1,903, $P = 0{\cdot}52$). Adults from Chernobyl weighed on average 1·1% less than adults from Kanev. Individuals with larger structural body size, as estimated by keel length, did not weigh more in Kanev (linear regression: males: $F = 0{\cdot}76$, d.f. = 1,179, $P = 0{\cdot}38$; females: $F = 0{\cdot}86$,

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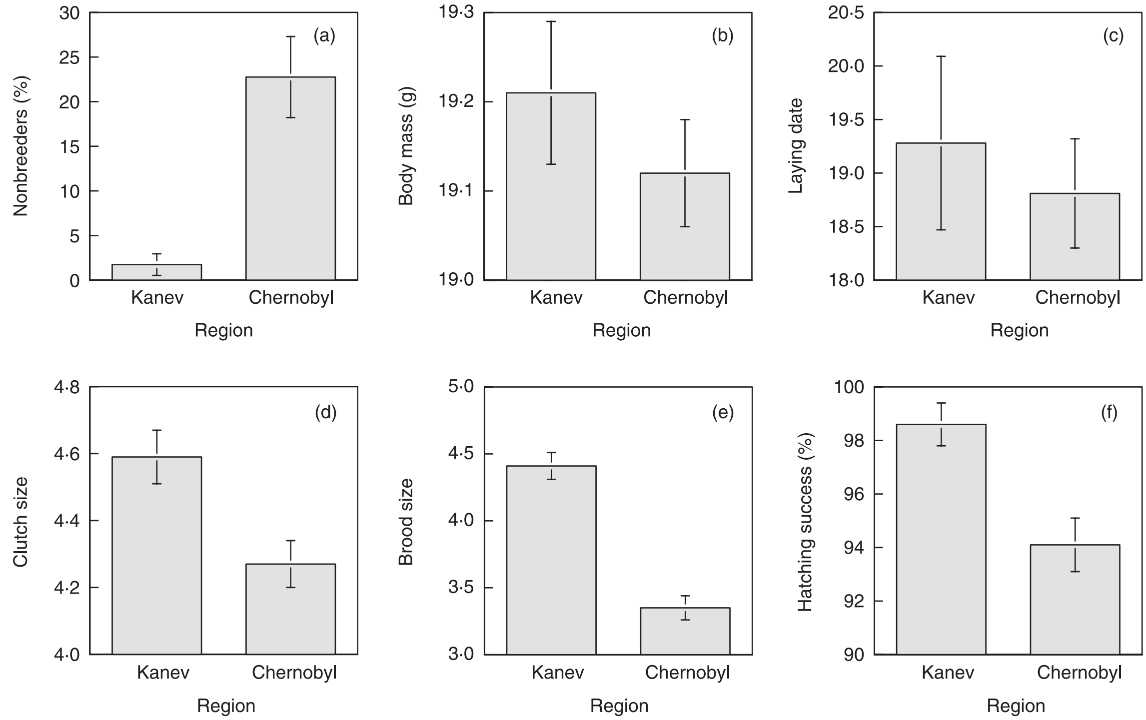

Fig. 2. Difference in (a) percentage nonbreeders (%), (b) body mass (g), (c) laying date (day 1 = 1 May), (d) clutch size, (e) brood size and (f) hatching success (%) between Chernobyl and Kanev regions. Values are means (±SE).

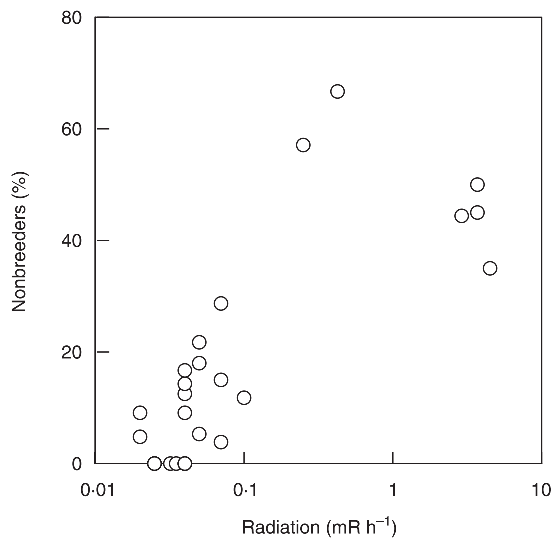

Fig. 3. Relationship between abundance of nonbreeding adult barn swallows (%) and level of radiation (mR h^{-1}) in Chernobyl and Kanev regions.

d.f. = 1,169, $P = 0{\cdot}35$), but did so in the Chernobyl region, particularly for females [linear regression: males: $F = 14{\cdot}53$, d.f. = 1,283, $r^2 = 0{\cdot}05$, slope (SE) = 0·03 (0·008), $P = 0{\cdot}002$; females: $F = 24{\cdot}21$, d.f. = 1,253, $r^2 = 0{\cdot}09$, slope (SE) = 0·05 (0·01), $P < 0{\cdot}0001$]. Barn swallows had slightly shorter keels in Chernobyl than in Kanev (mean difference of 1·0%), and this difference between areas was similar in the two sexes ($F = 0{\cdot}18$, d.f. = 1,888, $P = 0{\cdot}68$). An analysis of covariance with body mass as the dependent variable and region, sex, and region by sex as factors and keel length as a covariate did not reveal a significant effect of region on body mass ($F = 2{\cdot}54$, d.f. = 1,887, $P = 0{\cdot}11$). The relationship between mean body mass per colony and level of radiation was not statistically significant (Spearman rank correlation: $r_S = 0{\cdot}05$, $z = 0{\cdot}25$, $n = 31$, $P = 0{\cdot}81$).

REPRODUCTIVE RATES

Laying date did not differ significantly between the two regions (Fig. 2d; $F = 0{\cdot}23$, d.f. = 1,181, $P = 0{\cdot}64$). This finding was independent of year effects ($F = 0{\cdot}14$, d.f. = 1,177, $P = 0{\cdot}71$). Thus differences for clutch and brood size, and for hatching success, were independent of laying date effects. The relationship between mean laying date and radiation level was not statistically significant (Spearman rank correlation: $r_S = 0{\cdot}05$, $z = 0{\cdot}22$, $n = 23$, $P = 0{\cdot}83$).

Clutch size was 7·0% smaller in the Chernobyl region than in the Kanev region (Fig. 2e; $F = 6{\cdot}83$, d.f. = 1,217, $P = 0{\cdot}01$). This effect remained significant after accounting for year effects ($F = 5{\cdot}33$, d.f. = 1,213, $P = 0{\cdot}02$). Overall, the relationship between mean clutch size and radiation level was significantly negative (Spearman rank correlation: $r_S = -0{\cdot}49$, $z = 2{\cdot}28$, $n = 23$, $P = 0{\cdot}02$).

Brood size at hatching also was smaller in Chernobyl than in Kanev (Fig. 2f; $F = 17{\cdot}04$, d.f. = 1,176, $P < 0{\cdot}0001$), with a mean difference of 13·5%. This effect was independent of year ($F = 39{\cdot}95$, d.f. = 1,171, $P < 0{\cdot}0001$). The relationship between mean brood size and radiation level was also significantly negative (Spearman rank correlation: $r_S = -0{\cdot}59$, $z = 2{\cdot}79$, $n = 23$, $P = 0{\cdot}005$).

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Hatching success was significantly higher in Kanev than in Chernobyl (Fig. 2g; $F = 6{\cdot}42$, d.f. = 1,175, $P = 0{\cdot}01$) with a mean difference between regions of 4·6%. This effect was independent of year ($F = 7{\cdot}13$, d.f. = 1,171, $P = 0{\cdot}008$). There was also a significant negative relationship between mean hatching success and radiation level (Spearman rank correlation: $r_S = -0{\cdot}52$, $z = 2{\cdot}69$, $n = 23$, $P = 0{\cdot}007$).

One of our study sites (Vesniane) was within the exclusion zone, where farming ceased completely in 1986. Exclusion of this site from the analyses revealed very similar results, and none of the differences reported above changed after exclusion of data from Vesniane.

ANNUAL SURVIVAL RATE OF ADULTS

The basic Cormack–Jolly–Seber model (S_{g*t}, P_{g*t}) was used to fit the survival data ($\chi^2 = 0{\cdot}28$, d.f. = 2, $P = 0{\cdot}87$; RELEASE; $P = 0{\cdot}23$; 100 repetitions, deviance-based bootstrap goodness-of-fit (GOF) test by MARK). The overdispersion value (c-hat), estimated on the basis of the bootstrapped GOF, was slightly less than 1 (c-hat = 0·99), and a c-hat = 1-value was used during model selection.

In the global model we examined annual survival (S) and recapture rates (P) for four groups (g; males and females in Chernobyl and Kanev), and their interaction with study period (g ∗ t).

The two most parsimonious models differed little in their AICc scores (632·4, 632·64). Both models found significant differences between Chernobyl and control populations in recapture rates. The first model also suggested differences in recapture rates between males and females in the Chernobyl populations but not for the control regions. However, a LRT of these two models suggested there was no significant difference between the sexes in recapture rate in Chernobyl during the study period, although the power of this test was low ($\chi^2 = 2{\cdot}33$, d.f. = 1, $P = 0{\cdot}13$; LRT).

Recapture rate differed significantly among the studied groups, being lower for Kanev birds when compared with males and females in the Chernobyl area ($\chi^2 = 7{\cdot}58$, d.f. = 2, $P = 0{\cdot}02$; LRT).

Recapture rate also varied significantly among years ($\chi^2 = 13{\cdot}13$, d.f. = 2, $P = 0{\cdot}001$; LRT). There was no significant interaction among groups and years, causing the recapture rate to vary in parallel over the study period ($\chi^2 = 3{\cdot}72$, d.f. = 6, $P = 0{\cdot}72$; LRT).

On the basis of the LRTs of nested models we found that annual survival rates varied greatly among study groups and sexes [Chernobyl males: 0·327 (SE = 0·085); Chernobyl females: 0·233 (SE = 0·028); Kanev males: 0·431 (SE = 0·100); Kanev females: 0·542 (SE = 0·170); $\chi^2 = 18{\cdot}44$, d.f. = 2, $P < 0{\cdot}001$; LRT]. However, although differences between male and female survival rates were significant in the Kanev populations ($\chi^2 = 5{\cdot}56$, d.f. = 1, $P = 0{\cdot}02$; LRT), this was not the case for Chernobyl ($\chi^2 = 0{\cdot}12$, d.f. = 1, $P = 0{\cdot}73$; LRT).

Observed survival rates varied significantly among years in both regions in parallel (year effect: $\chi^2 = 14{\cdot}59$, d.f. = 2, $P < 0{\cdot}001$; in a parallel fashion: interaction between year and location: $\chi^2 = 2{\cdot}40$, d.f. = 6, $P = 0{\cdot}88$; LRT).

Discussion

Barn swallows in the Chernobyl region only differed slightly in body mass from barn swallows from the control area. Surprisingly, we found different patterns of body mass–body size relationships between the Chernobyl and Kanev regions. While body mass was independent of skeletal size (as estimated from keel length) in Kanev, as has been found in Denmark (Møller 1994), there were clear positive relationships in Chernobyl. This difference was particularly pronounced in females, while the difference for males was less clear. We hypothesize that this difference may partly be the result of effects of radiation on mutation. Small individuals in Chernobyl may be more likely to be mutants, which because of deleterious effects of mutations also have a small body mass (Møller & Mousseau 2001). In contrast, small individuals in Kanev are likely to be small for reasons other than deleterious mutations, and their body mass is therefore not likely to be reduced in comparison with the body mass of large individuals.

In the Chernobyl region a large fraction of the adult females were nonbreeders. Nonbreeding in the barn swallow has previously been recorded only in males, as a slightly skewed sex ratio results in on average 9·4% of males remaining unmated in a Danish population (Møller 1988, 1994; A. P. Møller, unpublished data). The large proportion of nonbreeding females recorded in several colonies in the Chernobyl region is unprecedented in the numerous studies of barn swallows in Europe (e.g. Møller 1994). Thus, the observed frequency of 22·8% (SE = 4·5) nonbreeding females in Chernobyl is well above the level recorded in the control area in Kanev of 1·7% (SE = 1·2) (Fig. 2a). It is also well above the null expectation of 0% nonbreeding females based on data from three long-term studies of barn swallows in Denmark, Italy and Spain of each more than 3000 individually banded adult barn swallows (A. P. Møller, F. de Lope & N. Saino, unpublished data). However, the estimate from Kanev did not deviate significantly from the value recorded in the west European populations. This suggests that nonbreeding among females was markedly higher in Chernobyl than in Kanev. In contrast, the adult sex ratio in Chernobyl did not differ from that recorded in Denmark (Møller 1994), or from that recorded in Kanev. Thus, elevated levels of radiation in Chernobyl were not associated with a difference in adult sex ratio.

Among the barn swallows that bred, clutch size and in particular brood size were small, with a smaller fraction of eggs hatching in Chernobyl than in Kanev. There was no significant difference in laying date between the two regions, suggesting that this variable was not a confounding factor for differences in clutch size, brood size or hatching success.

Adult survival in the Chernobyl region was also low compared with the control area in Ukraine and to estimates from western Europe (Møller 1994; Møller & Szép 2002; A. P. Møller, T. Szép, N. Saino & F. de Lope, unpublished data). The population in the Chernobyl area therefore decreased considerably, while that was not the case in the control area near Kanev. Numerous studies of the breeding biology of European barn swallows have revealed clear geographical patterns with laying being later and clutch sizes larger towards the north (Møller 1984, 1994). As the Chernobyl region is *c*. 250 km further north than the Kanev region, the results are conservative as we would expect a priori that laying would be later and clutches larger in the Chernobyl region. They clearly were not.

The recorded survival rates and reproductive rates in the Chernobyl region are not sufficient to maintain a stable population size. If we assume that the population in the Kanev region is self-sustaining, then the population in Chernobyl clearly cannot be sustained without immigration. Adult survival rate in Chernobyl was only 43% of that in the Kanev region for females and 76% for males. While 23% of adult females were nonbreeders in the Chernobyl region, less than 2% were nonbreeders in the Kanev region. In addition, brood size was more than 24% lower in Chernobyl than in Kanev. A study of a decreasing Danish barn swallow population with an adult survival rate of 35% revealed that the population was not sustainable even though the reproductive rate was higher than that recorded in the Chernobyl region (Engen, Sæther & Møller 2001). Thus, the Chernobyl population cannot possibly be sustainable and must be acting as a sink population.

We can only speculate about the possible mechanisms generating the observed patterns described here. Here we propose two different, but not necessarily mutually exclusive explanations: (1) deleterious effects of mutations, and (2) negative effects of radiation on antioxidants. This study did not provide analyses that allow us to assess the relative role of mutations and use of antioxidants as a cause of the reduction in reproductive rate and annual adult survival. Also, alternative interpretations exist. The observations reported here may be accounted for if there were differences in abundance or composition of food between the two regions. Barn swallows mainly feed on Diptera, particularly Muscidae, Syrphidae and Tabanidae, but also aphids, beetles and butterflies (Møller 1994). Barn swallows must ingest all antioxidants, and carotenoids are particularly common in insects that feed on pollen such as Syrphidae and Lepidoptera, but also in insects that feed on leaves such as aphids and caterpillars. As most radionuclides (mainly Cs^{137} and Sr^{90}) are in the upper soil (Shestopalov 1996), we might expect Diptera to be more affected by radiation than aphids or Lepidoptera. Hence, there is no reason to expect differences in carotenoid availability due to differences in the abundance of insects to account for the reported findings.

A second alternative is that changes in farming practice differ between the two regions. Modern farming has collapsed in the large collective farms and the number of dairy cows have been reduced dramatically. For example, the number of dairy cows in two large farms in the Chernobyl and Kanev regions has decreased from 250 and 230 in 1991, respectively, to 30 and 38 cows in 2002. Clutch size of barn swallows in Denmark is slightly smaller (on average 4·9%) on farms without than with cows, while there are no effects of abandonment of dairy farming on adult body mass, frequency of nonbreeding, hatching success, brood size or adult survival (Møller 2001). Changes in farming practice are very similar across Ukraine and thus cannot account for the regional differences or the patterns observed within the regions described here. Although large areas in the Chernobyl region have been depopulated and farming has ceased completely as an official measure to reduce transfer of radioactive material to humans through food, this cannot have affected our results because we almost exclusively worked outside the exclusion zone. Only one of our study sites was within the exclusion zone, and our general findings did not change after exclusion of this single observation. Hence, it is unlikely that environmental changes can account for the observations reported here, as changes in agricultural practice have been similar across Ukraine. Finally, both alternative explanations would suggest large differences in body condition of adults between areas, which was clearly not the case.

Why are the associations between radiation, condition, reproduction and survival so clear in the barn swallow? First, we do not know whether similar patterns will be found in other avian species, as no other studies have been made to date. Second, if the patterns reported for the barn swallow turn out to be unique, we suggest that antioxidants may be the cause. Migratory birds that fly thousands of kilometres produce large amounts of free radicals that must be neutralized by antioxidants (Ninni *et al*. 2004). In addition, females allocate considerable amounts of antioxidants to eggs (Blount, Houston & Møller 2000; Blount *et al*. 2003), resulting in a second minimum in body antioxidants during a short period of time. Given that large amounts of antioxidants are used for coping with the physiological consequences of radiation in the Chernobyl region (Chaialo *et al*. 1991; Bazhan 1998; Ben-Amotz *et al*. 1998; Ivaniota *et al*. 1998; Neyfakh *et al*. 1998a,b; Lykholat & Chernaya 1999; Kumerova *et al*. 2000; Møller *et al*. 2005), there may be trade-offs between allocation to competing demands such as those caused by migration and reproduction.

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