

Demography of population recovery: survival and fidelity of peregrine falcons at various stages of population recovery

George D. Smith · Oscar E. Murillo-García ·
Jeffrey A. Hostetler · Richard Mearns · Chris Rollie ·
Ian Newton · Michael J. McGrady · Madan K. Oli

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Abstract Factors influencing vital demographic rates and population dynamics can vary across phases of population growth. We studied factors influencing survival and fidelity of peregrine falcons in south Scotland—north England at two stages of population growth: when the population was recovering from pesticide-related declines and density was low, and when it had largely recovered from pesticide effects and density was high. Fidelity was higher for: adults and subadults than for juveniles, females than for males, and juveniles and adults during the low-density than during the high-density study period. Survival was age specific,

with lower survival for juveniles than for older birds (juveniles, $0.600 \pm \text{SE } 0.063$; subadults, 0.811 ± 0.058 ; adults, 0.810 ± 0.034). Furthermore, there was some evidence that survival was generally lower for all age classes during the low-density period than during the high-density period, possibly due to a chronic, persistent effect of organochlorine pesticides as the population recovered. Evidence for a density-dependent effect on survival was weak, but a negative effect of density on fidelity of juveniles (dispersing age class) during the recovery phase suggests density-dependent dispersal when the population was increasing. Our results show how population density can influence demographic parameters differently and how such influences can vary across phases of population growth.

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G. D. Smith
Scottish Raptor Study Group, 58 Meadowbank Road,
Kirknewton, West Lothian EH27 8BS, UK

O. E. Murillo-García · M. K. Oli
School of Natural Resources and Environment,
University of Florida, Gainesville, FL 32611, USA

O. E. Murillo-García · M. K. Oli (✉)
Department of Wildlife Ecology and Conservation,
University of Florida, 110 Newins-Ziegler Hall,
Gainesville, FL 32611-0430, USA
e-mail: olim@ufl.edu

Present Address:
O. E. Murillo-García
Departamento de Biología, Universidad del Valle, Cali, Colombia

J. A. Hostetler
Migratory Bird Center, Smithsonian Conservation Biology
Institute, National Zoological Park, Washington, DC, USA

R. Mearns
Conansknowe, Kirkton, Dumfries DG1 1SX, UK

C. Rollie
Royal Society for the Protection of Birds, Dumfries
and Galloway Office, The Old School, Crossmichael,
Castle Douglas DG7 3AP, UK

I. Newton
Centre for Ecology and Hydrology, Benson Lane,
Crowmarsh Gifford, Wallingford OX10 8BB, UK

M. J. McGrady
International Avian Research, Am Rosenhügel 59,
3500 Krems, Austria

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Introduction

It is now more than 50 years since Rachel Carson (Carson 1962) summarized what would turn out to be devastating effects of organochlorine pesticides, including dichlorodiphenyl-trichloroethane (DDT), aldrin, dieldrin and others, on avian populations, thus marking for many the beginning of the environmental movement in modern times. It soon became evident that chemical pesticides were affecting not just songbirds but many forms of life, and the effect was global in scope (Hunter 1967; Ratcliffe 1970; Bloom et al. 1979; Newton 1986). It is generally believed that the widespread use of organochlorine pesticides was the primary cause of global population declines of many species of raptorial and fish-eating birds that occurred during 1947–1975 (Ratcliffe 1970, 1993; Newton 1979, 1986). Dichloro-diphenyl-dichloroethylene (DDE; a derivative of DDT) and DDT can bio-accumulate and cause eggshell thinning in some species of birds, which in turn leads to reduced reproductive success due to inability to lay eggs, egg breakage, and death of the embryos (Ratcliffe 1970; Cooke 1979; Newton 1979). Cyclodene compounds such as dieldrin, on the other hand, are more toxic than DDT/DDE and can increase mortality above natural levels (Prestt and Ratcliffe 1967; Newton 1979, 1998; Hudson et al. 1984; Nisbet 1988). The effects of various pesticides and their relative contributions to raptor population declines varied in different parts of the world, some populations being affected mainly by DDT-induced reproductive failure and others mainly by dieldrin-induced mortality (Newton 1979; Nisbet 1988; Stone and Okoniewski 1988).

The breeding population of peregrine falcons (*Falco peregrinus* L.; hereafter ‘peregrine’) of Britain and Ireland had declined by 1963 to approximately 44 % of the level estimated for 1930–1939 (Ratcliffe 1993). Territory desertion, failure of eggs to hatch, egg breaking, small broods and territory occupancy by single birds characterized population declines (Cade et al. 1988). Such declines were observed throughout the world wherever organochlorine pesticides were commonly used (Cade et al. 1988). British ornithologists concluded that adult mortality caused by aldrin-dieldrin was the most important cause of decline of peregrines and other birds of prey in the UK (Ratcliffe 1970, 1988; Newton 1986), though other factors such as DDT-induced shell thinning, egg collecting and direct persecution also played a part. In contrast, reproductive failure caused by DDE was considered as the main cause of peregrine population declines in North America (Cade et al. 1988). Evidence about the primary mechanisms underlying

organochlorine—related declines in raptor populations is based partly on circumstantial evidence of temporal and geographical correlations between the declines in numbers, shell thickness and nest success and organochlorine use, and partly on experimental results obtained by feeding organochlorine-laced food to captive birds (Newton 1979; Cade et al. 1988).

Once the devastating effect of organochlorine pesticides on wildlife was established, their use was progressively reduced, and in many countries, banned completely (Cade et al. 1988). Populations of affected bird species then recovered at varying rates (Wyllie and Newton 1991; Newton and Wyllie 1992; Newton 1998; Banks et al. 2010). By 2000, the British population of peregrines had fully recovered naturally from the deleterious effects of organochlorine pesticides, although reductions in territory occupancy rates were subsequently reported from parts of Scotland, associated with an increase in human persecution (Banks et al. 2010).

We studied factors influencing survival and fidelity to study site of peregrines in south Scotland—north England in two periods: when they were still affected but recovering from the pesticide-related decline, and when the population had recovered. The peregrine population in our study area was low in the 1970s, but increased steadily until reaching a high density by the early 2000s (Banks et al. 2010; Smith and McGrady, unpublished data). We applied live-recapture dead-recovery models (Burnham 1993) to data collected in south Scotland—north England during the recovery phase (1974–1982) and during the high-density phase (2002–2011). By applying that modelling framework to detailed live-recapture dead-recovery data collected at two phases of population growth, we were able not only to estimate age- and sex-specific survival and fidelity rates for each study period, but also to test predictions regarding factors influencing these rates at different phases of population growth.

We tested six predictions related to peregrine survival and fidelity to the study area:

1. Fidelity would be lower for juveniles than for older age classes and lower for females than for males. Juveniles were more likely to move longer distances than older age classes, on average, before they found a place to settle (Ratcliffe 1993), and a lower fidelity is expected for females than for males because a greater proportion of females than males moved long distances, and also a greater proportion of breeding males than breeding females had hatched within the study area (Mearns and Newton 1984).
2. Fidelity would be lower for juveniles during the (latter) high-density study period because fidelity of the dispersing age class (pre-breeders) would be negatively

affected by density; high population density would lead to a shortage of territories, forcing dispersers to settle outside of the study area.

3. The annual survival rate would be lower for juveniles than for older age classes because this is generally true for raptors (Newton 1979).
4. Annual survival would be lower for males because they are smaller and body size is generally positively related to survival (Newton 1979).
5. Survival rates would differ between the two stages of population growth, and they would be negatively affected by density (Clutton-Brock et al. 1987; Newton 1998).
6. Survival would be negatively affected by an increase in monthly average rainfall, an increase in days of air frost, and/or a decrease in monthly temperatures (maximum and minimum) November–April. Heavy rain and low temperatures can make hunting by peregrines more difficult, and perhaps make the birds more susceptible to diseases, shooting and accidents.

Materials and methods

Study area and population monitoring

The study area is located in south Scotland—north England, south of Edinburgh and Glasgow, extending into the Kielder Forest area of Northumberland (Fig. 1). There is a long history of monitoring of peregrine breeding sites in this region, and for some territories, experienced ornithologists have collected data annually since the early 1960s. The landscape is hilly, coastal in the east and west rising to maximum elevations of about 500–700 m. inland. This region is characterized by mixed farming on the lower ground, with pasture and arable land, and by open grassy sheepwalk, heather (*Calluna vulgaris*) moor, and plantations of mostly exotic conifers (e.g. *Picea sitchensis*) on the higher ground. Peregrines are resident and feed on a variety of avian prey, but racing and feral pigeons (*Columba livia*) are a particularly important food source (Ratcliffe 1993).

In the first study period (1974–1982), the population density was low [mean index of relative density 0.469 ± 0.049 (SE) pairs/km²; see “Statistical analyses” section for details] and still recovering from the pesticide-related decline (hereafter, ‘earlier period’ or ‘low-density period’), and in the second period (2002–2011), the population had recovered to high density (mean index of relative density, 0.875 ± 0.022 pairs/km²), comparable to pre-decline levels, and was considered to be stable (hereafter, ‘latter period’ or ‘high-density period’). Although the sampling area during the two study periods did not completely overlap, the latter study sampled almost all of the area

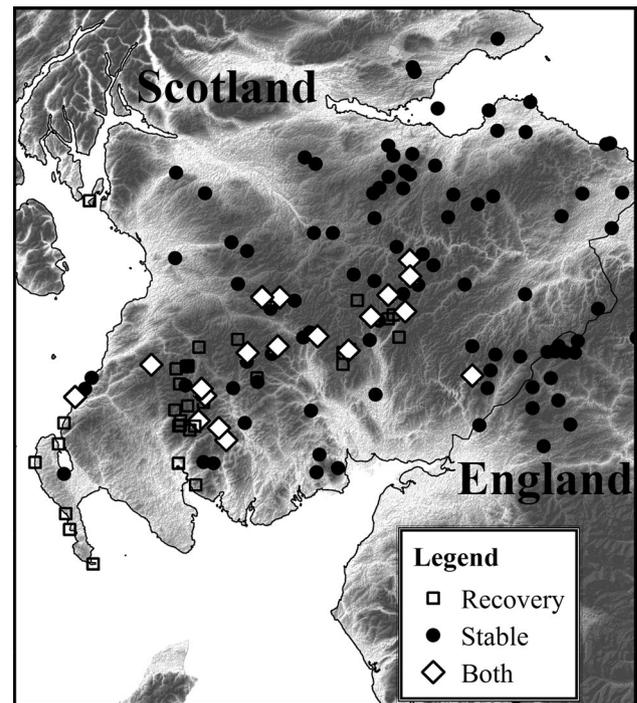


Fig. 1 The south Scotland—north England study area, showing locations of peregrine falcon territories monitored during the two study periods: earlier or low-density (1974–1982) and later or high-density (2002–2010) period

embraced by the earlier one and also covered areas that were unoccupied by peregrines during the earlier study.

Peregrines in our study area were sampled intensively during both study periods. During the earlier study period, birds were marked with rings under the British Trust for Ornithology (BTO) scheme (Baillie et al. 1999), and attempts were made every year to catch as many breeders on territories as possible, prioritising territories where birds had been caught in previous years (Mearns and Newton 1984, 1988; Newton and Mearns 1988). During the latter period, in addition to BTO rings, breeding and nestling peregrines were fitted with passive integrated transponder (PIT) rings. PIT rings allowed breeding birds to be electronically identified when they returned to incubate eggs, brood or feed young, without the need to capture them, and increased the number of individuals identified of both sexes.

Trapping was not practical at all territories because some cliffs were remote or inaccessible, especially coastal ones. Records of birds, marked in our study area during both study periods and found dead or injured, were provided from our own fieldwork within the study area and reported by members of the public to the BTO, so in theory they could have come from anywhere in Britain and Ireland (none were reported from continental Europe).

Newton and Mearns (1988) reported minimal annual survival rates based on the data collected during the low-density (earlier) study period, calculated as the proportion of birds caught in any one year that were re-caught in a later year. We re-analysed those data using a capture-recapture and recovery framework that allowed us to estimate annual survival and fidelity to the study area of peregrines during that study period. In addition, we applied the same modelling framework to the latter study period, so we were able to compare inferences and estimates of survival rates of peregrines between both phases of population growth.

Statistical analyses

We applied a live-capture dead-recovery modelling framework to estimate and model survival and fidelity to study site. We used Burnham's model (Burnham 1993), which consists of four parameters: probability of capture (p), probability of recovery (r ; probability that a dead bird is recovered and reported), true survival (S), and fidelity (F ; the probability that an individual in the study area at time i is also in the study area at time $i + 1$, given that it is alive at $i + 1$). For parameter estimation and modelling, we distinguished three age classes: juveniles (first-year birds), subadults (second-year birds), and adults (birds more than 2 years of age). Our study years were 'biological', not calendar, years; they covered from spring to spring of consecutive years (i.e. 2009 covered the period between 1 April 2009 and 31 March 2010). Young peregrines do not fledge until late June–July; thus, survival of juveniles is not annual because it only covers 9–10 months. For estimation and modelling of survival, we only included capture and recapture data collected until 2011, but recovery data collected until 2010 because recoveries for 2011 were not available.

In our analyses, we considered several covariates including age, sex, study period, time (i.e. year) and climatic variables. If one allows the four estimable parameters of the Burnham model (p , r , F and S) to be affected by biologically meaningful independent, additive, and interactive effects of these covariates, one ends up with a large number of models some of which may differ only in model structures for the nuisance parameters (p and r); this would make statistical inference regarding the primary parameters of interest (F and S) difficult. To avoid this difficulty, we used a sequential approach to data analysis (MacKenzie et al. 2010). First, we fixed S to the interactive effect of age and sex [$S(\text{sex} \times \text{age})$] and allowed p , r and F to be affected by age, sex, time (year), study period, and biologically meaningful additive and interactive (two-way interactions) effects of these variables. This led to a set of models, many of which differed only in model structures for r and p ; this made statistical inference and test of our hypotheses difficult. We therefore ran a reduced set of models with r

and p fixed at the top model structures identified for each parameter in the preceding analyses, and F was allowed to vary as before. To test whether (and to what extent) restricting model structure as described affected model ranking and hypothesis testing, we ran the reduced model sets for F with the two best model structures for r and p . Second, we fixed model structure for F to that identified as the best structure in preceding analyses, and repeated the above process to identify the best model structure for S . Because the top two models for F were equally supported by data, we repeated the above analyses with F fixed at the second-best model structure.

Using the best base models from preceding analyses, we tested for the effects of environmental factors hypothesized to influence peregrine survival in a density-independent manner. We hypothesized that weather variables might influence peregrine survival during the winter and early spring months when weather was sometimes harsh (November–March). Thus, we considered the effect on annual survival of mean daily maximum temperature (t_{max}), mean daily minimum temperature (t_{min}), total rainfall (rain) and days of air frost (af) for each individual month, and for the whole November–March period (from Eskdalemuir Weather Station, located near the centre of our study area, <http://www.metoffice.gov.uk/climate/uk/>, accessed 15 January 2012). To test for winter (rather than monthly) effect of weather variables, we also tested for the effect of total rainfall, minimum and maximum daily temperature and days of air frost over the period November–March on survival. Finally, we tested for density-dependent effects on survival of peregrines by allowing survival rates to be affected by an index of density with and without a time lag of 1 year. To estimate the size of the sampled area, we first determined locations of all nest sites surveyed during each study period. We then estimated the approximate sampling area as the 90 % minimum convex polygon using the R package *adehabitat* version 1.8.12 (Calenge 2006). Year-specific index of relative density was then estimated for each study period by dividing the number of peregrine breeding pairs during each year by the respective size of the sampled area.

We used Akaike's information criterion corrected for small sample size (AICc) for model selection and statistical inference regarding factors influencing all model parameters (Burnham and Anderson 2002). Differences in AICc (ΔAICc) and AICc weights were computed for all candidate models and used to assess the relative support they received from data (Burnham and Anderson 2002). Models that could not estimate ≥ 1 parameters were excluded for model comparison and for computing model-averaged parameter estimates. Analyses were implemented in program MARK (White and Burnham 1999) using the package RMark (Laake 2013) in the R 2.2.14 computing environment (R Development Core Team 2012).

Table 1 Model comparison table for Burnham live-recapture and dead-recovery analysis to determine the best base model for fidelity (*F*) of peregrine to the south Scotland—north England study area, and to test for the effects of index of population density on *F*

No.	Model	<i>K</i>	AICc	ΔAICc	Weight
(a) $p(\text{age} + \text{period})r(\text{time} \times \text{period})$					
1	$F(\text{sex} + \text{age} + \text{period})$	18	35,062.125	0.000	0.376
2	$F(\text{sex} \times \text{period} + \text{age})$	19	35,062.861	0.736	0.260
3	$F(\text{sex} \times \text{period} + \text{age} \times \text{period})$	21	35,063.615	1.490	0.179
4	$F(\text{sex} + \text{age} \times \text{period})$	20	35,064.413	2.288	0.120
5	$F(\text{sex} \times \text{age} + \text{period})$	20	35,065.840	3.715	0.059
(b) $p(\text{sex} + \text{age} + \text{period})r(\text{time} \times \text{period})$					
1	$F(\text{sex} + \text{age} + \text{period})$	19	35,062.506	0.000	0.402
2	$F(\text{sex} \times \text{period} + \text{age} \times \text{period})$	22	35,062.828	0.322	0.342
3	$F(\text{sex} + \text{age} \times \text{period})$	21	35,064.381	1.875	0.157
4	$F(\text{sex} \times \text{age} + \text{period})$	21	35,066.263	3.757	0.061
5	$F(\text{age} \times \text{period})$	20	35,067.301	4.796	0.037
(c) $p(\text{age} \times \text{period})r(\text{time} \times \text{period})$					
1	$F(\text{sex} + \text{age} + \text{period})$	19	35,063.686	0.000	0.443
2	$F(\text{sex} \times \text{period} + \text{age})$	20	35,064.454	0.769	0.302
3	$F(\text{sex} \times \text{period} + \text{age} \times \text{period})$	22	35,065.483	1.797	0.180
4	$F(\text{sex} \times \text{age} + \text{period})$	21	35,067.433	3.747	0.068
(d) Models testing for the effect of density					
1	$F[(\text{sex} + \text{age} + \text{period}) \times \text{density}_{t-1}]$	23	35,051.350	0.000	0.961

We ran three sets of models, using the three top models for *p* and *r* (a–c); for these analyses, survival rate (*S*) was fixed to the interactive effect of age and sex. We tested for the effect of sex (males and females), age (juveniles, <1 year old; subadults, 1–2 years old; adults, >2 years old), study period (*period*; recovery, 1974–1982; stable, 2002–2010), and a linear temporal trend (*time*) on *F*. We used the best base model for *F* (model 1; Table B2) to test for the effects of (d) index of population density. Best-supported models [difference in Akaike’s information criterion corrected for small sample size (ΔAICc < 5)] are presented for each model set. The table includes the number of parameters (*K*), AICc, ΔAICc and model weights (relative likelihood of models in the set)

Density_{t-1} Density of breeding pairs in year *t* – 1

Results

Some 461 individuals (417 juveniles and 44 adults) were marked, and 103 recaptures (55 individuals) were registered during the first study period (recovery period; 1973–1982). During the second study period (stable period; 2002–2011), some 730 individuals (621 juveniles and 109 adults) were marked and 180 recaptures (72 individuals) were registered. A detailed summary of sex and age composition of peregrines in our data set is presented in Table A1 (Online Resource).

When *p*, *r* and *F* were allowed to vary with age, sex, time (year), a linear temporal trend (Time), study period,

and biologically meaningful additive and interactive effects of these variables, the best-supported model was ($\{p(\text{age} + \text{period})r(\text{time} \times \text{period})F(\text{sex} + \text{age} + \text{period})\}$) (Table A2, Online Resource). However, there was considerable uncertainty regarding the best model structures for *p* and *r*. *p* was more influenced by age (cumulative model weight = 1.000) and study period (cumulative model weight = 0.959) than by sex (cumulative model weight = 0.512) and time (cumulative model weight = 0.001). In general, model averaged estimates showed that *p* was higher for adults than for subadults, and higher for the recovery than for the stable study period (Table A3, Online Resource); we could not estimate *p* for juveniles because they were never recaptured again as juveniles. On the other hand, there was evidence that *r* differed between the two study periods (cumulative model weight = 1.000) and varied linearly with time (cumulative model weight = 0.998). The *r* was higher during the period of low density than during the high-density period, and declined linearly for both study periods (Table A4, Online Resource). Despite some uncertainty regarding the best model structures for *p* and *r*, two models for *p* [$p(\text{age} + \text{period})$ and $p(\text{sex} + \text{age} + \text{period})$] and one model for *r* [$r(\text{time} \times \text{period})$] dominated the top models for these parameters. We therefore ran three sets of reduced models for *F*, with *p* and *r* fixed to these structures.

There was strong evidence for an additive effect of age, sex and study period on fidelity rates (*F*) [model 1 (a–c); Table 1]. Based on that model, there was evidence that *F* was lower for juveniles than for older individuals, higher for females than for males and higher for the earlier than for latter study period (Fig. 2). A model that included age and interaction between sex and study period on *F* was also well supported [model 2 (a, c); Table 1]. Estimates based on this model suggested that subadults and adults had higher *F* than juveniles, and that juvenile and adult *F* differed between the study periods and sexes, with a higher *F* for females than for males during the recovery than the stable period. Population density in the previous year negatively influenced *F* of juveniles only during the earlier study period [females, $\beta = -11.63$, 95 % confidence interval (CI) = –18.33 to –4.93; males, $\beta = -13.50$, 95 % CI = –22.29 to –4.71], providing evidence for density dependence in *F* of the main dispersing age class [model 1 (d); Table 1]. The top model for *F* was the same, and model selection results were almost identical, in all three subsets that differed in model structures for *p* [(a–c); Table 1], with no appreciable differences among subsets regarding model structure or estimates of *F*. We therefore fixed model structure for *F* to an additive effect of sex, age and study period in order to model and estimate survival.

The models that included an effect of age on survival had the highest empirical support; this result was consistent

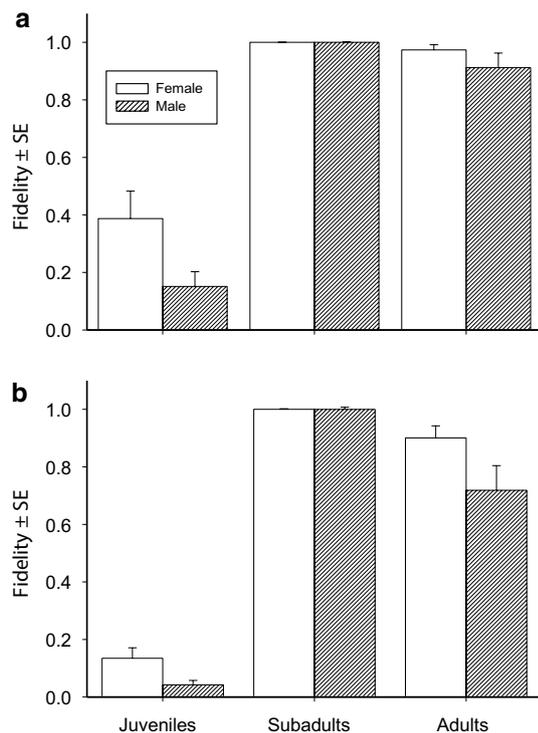


Fig. 2 Age- and sex-specific fidelity rates (F) (\pm SE) of peregrines in south Scotland–north England during the two study periods: **a** low-density (1974–1982) and **b** high-density (2002–2010). Estimates were based on the most parsimonious model that included an additive effect of age, sex and study period on survival [model 1 (a); Table 1]. Age classes are: <1 year, juveniles; 1–2 years, subadults; and >2 years, adults

across all three-model sets that differed in model structure for p [model 1 (a–c); Table 2], providing strong evidence for age-specific variation in survival. Based on the best model [model 1 (a); Table 2], survival was higher for adults and subadults than for juveniles (Fig. 3a). Models that included an additive effect of age and study period on survival also received substantial support [models 2 (a–c); Table 2]. Based on these models, survival was higher for adults and subadults than for juveniles, and was lower for the low-density (or earlier) period than for the high-density (or latter) study period (Fig. 3b, c). The top model for S was the same, and model selection results were almost identical [(a–c); Table 2], with no appreciable differences among subsets regarding model structure or estimates of S .

We tested for the effects of climatic covariates on survival using the most parsimonious model for all parameters [model 1 (a); Table 2] as a base model. A model that included an additive effect of rainfall in March on age-specific survival [model 1 (d); Table 2] was better supported ($>2 \Delta AIC_c$) than the base model [model 2 (d); Table 2], providing evidence for effects of rainfall on survival. Based on that model, the increase of total rainfall in March was

positively associated with survival; however, 95 % CIs for the slope parameter included zero (slope parameter, $\beta = 0.0051$, 95 % CI = -0.0004 to 0.0106), suggesting no statistically discernible effect of this variable. In addition, a model that included an interactive effect of March mean daily minimum temperature on age-specific survival [model 1 (e); Table 2] was better supported than the base model [model 2 (e); Table 2]. Based on that model, the increase of minimum temperature in March was positively associated with the annual survival of subadults ($\beta = 0.8809$, 95 % CI = 0.1845 – 1.5773), but not that of the other age classes (juveniles, $\beta = -0.1235$, 95 % CI = -0.4353 to 0.1884 ; adults, $\beta = -0.1631$, 95 % CI = -0.6254 to 0.2993). No other climatic variable we considered was substantially associated with survival. Analysis testing for the effect of winter weather variables revealed that the base model was better supported compared to models that included additive or interactive effects of winter rainfall, temperature or air frost [(g–i); Table 2]. Consequently, there was no evidence that the weather variables at seasonal scales (winter) had any influence on survival of peregrines in south Scotland–north England. Finally, there was no evidence that density, with or without a time lag, affected survival of any age class [(j); Table 2]; thus, there seemed to be no density-dependent effects on survival rates. Model-averaged estimates of F and S are presented in supporting information (Tables A5, A6, Online Resource).

Discussion

Arguably, the dynamics of biological populations are determined by both density-dependent and -independent processes (Tinbergen et al. 1985; Newton 1998). However, the relative influence of density-dependent and -independent factors on population dynamics can vary depending on the stage of population growth (Coulson et al. 2000; Goswami et al. 2011). Identifying such influences can be challenging since it would require long-term studies across different phases of population growth. Populations recovered after human-caused declines offer a unique opportunity to explore the changing roles of various factors influencing demographic parameters, and thus, population dynamics. Our goal was to examine factors and processes influencing fidelity and survival rates of peregrines during two phases of population growth: low-density phase when the population was recovering following organochlorine pesticide-caused declines, and high-density phase following population recovery to pre-decline levels.

As expected, fidelity to area was higher for adults and subadults than for juveniles, and was higher during the low-density period than during the high-density period for juveniles and adults. Peregrines disperse as juveniles

Table 2 Model comparison table for Burnham live-recapture and dead–recovery analysis of peregrines to determine the best base model for S in south Scotland—north England, and to test for the effects of climatic covariates and index of population density on S

No.	Model	K	AICc	Δ AICc	Weight
(a) $p(\text{age} + \text{period})r(\text{period} \times \text{time})$					
1	$S(\text{age})$	15	35,058.700	0.000	0.361
2	$S(\text{age} + \text{period})$	16	35,060.139	1.439	0.176
3	$S(\text{sex} + \text{age})$	16	35,060.596	1.896	0.140
4	$S(\text{sex} + \text{age} + \text{period})$	17	35,061.801	3.101	0.077
5	$S(\text{age} \times \text{period})$	18	35,061.847	3.147	0.075
6	$S(\text{sex} \times \text{age})$	18	35,062.125	3.425	0.065
7	$S(\text{age} \times \text{period} + \text{sex})$	19	35,063.554	4.854	0.032
8	$S(\text{sex} + \text{age} \times \text{period})$	19	35,063.554	4.854	0.032
(b) $p(\text{age} + \text{sex} + \text{period})r(\text{period} \times \text{time})$					
1	$S(\text{age})$	16	35,059.245	0.000	0.343
2	$S(\text{age} + \text{period})$	17	35,060.587	1.342	0.175
3	$S(\text{sex} + \text{age})$	17	35,061.111	1.866	0.135
4	$S(\text{sex} + \text{age} + \text{period})$	18	35,062.118	2.873	0.082
5	$S(\text{age} \times \text{period})$	19	35,062.152	2.907	0.080
6	$S(\text{sex} \times \text{age})$	19	35,062.506	3.261	0.067
7	$S(\text{age} \times \text{period} + \text{sex})$	20	35,063.783	4.538	0.035
8	$S(\text{sex} + \text{age} \times \text{period})$	20	35,063.783	4.538	0.035
9	$S(\text{sex} \times \text{period} + \text{age})$	19	35,064.163	4.918	0.029
(c) $p(\text{age} \times \text{period})r(\text{period} \times \text{time})$					
1	$S(\text{age})$	16	35,060.269	0.000	0.376
2	$S(\text{age} + \text{period})$	17	35,061.856	1.587	0.170
3	$S(\text{sex} + \text{age})$	17	35,062.160	1.891	0.146
4	$S(\text{sex} + \text{age} + \text{period})$	18	35,063.537	3.268	0.073
5	$S(\text{age} \times \text{period})$	19	35,063.685	3.416	0.068
6	$S(\text{sex} \times \text{age})$	19	35,063.686	3.417	0.068
(d) Models testing for the effect of rainfall					
1	$S(\text{age} + \text{rain.Mar})$	16	35,057.65	0.00	0.29
2	$S(\text{age})$	15	35,058.70	1.05	0.17
3	$S(\text{age} + \text{rain.Dec})$	16	35,058.91	1.26	0.15
4	$S(\text{age} + \text{rain.Nov})$	16	35,059.99	2.34	0.09
5	$S(\text{age} \times \text{rain.Mar})$	18	35,060.67	3.02	0.06
6	$S(\text{age} + \text{rain.Feb})$	16	35,060.72	3.07	0.06
7	$S(\text{age} \times \text{rain.Nov})$	18	35,061.05	3.40	0.05
8	$S(\text{age} \times \text{rain.Dec})$	18	35,061.16	3.51	0.05
9	$S(\text{age} \times \text{rain.Jan})$	18	35,061.67	4.03	0.04
10	$S(\text{age} \times \text{rain.Feb})$	18	35,062.24	4.59	0.03
(e) Models testing for the effect of temperature					
1	$S(\text{age} \times t_{\text{min.Mar}})$	18	35,054.73	0.00	0.51
2	$S(\text{age})$	15	35,058.70	3.97	0.07
3	$S(\text{age} + t_{\text{min.Jan}})$	16	35,059.33	4.60	0.05
4	$S(\text{age} \times t_{\text{min.Jan}})$	18	35,059.41	4.68	0.05
5	$S(\text{age} \times t_{\text{max.Jan}})$	18	35,059.67	4.94	0.04
(f) Models testing for the effect of days of air frost					
1	$S(\text{age})$	15	35,058.70	0.00	0.24
2	$S(\text{age} + \text{af.Dec})$	16	35,058.77	0.07	0.23
3	$S(\text{age} + \text{af.Nov})$	16	35,059.94	1.24	0.13
4	$S(\text{age} + \text{af.Feb})$	16	35,060.46	1.76	0.10

Table 2 continued

No.	Model	<i>K</i>	AICc	Δ AICc	Weight
5	$S(\text{age} + \text{af.Jan})$	16	35,060.52	1.82	0.10
6	$S(\text{age} + \text{af.Mar})$	16	35,060.69	1.99	0.09
7	$S(\text{age} \times \text{af.Dec})$	18	35,061.74	3.04	0.05
8	$S(\text{age} \times \text{af.Mar})$	18	35,063.15	4.45	0.03
9	$S(\text{age} \times \text{af.Jan})$	18	35,063.46	4.76	0.02
(g) Models testing for the effect of winter rainfall					
1	$S(\text{age})$	15	35,058.70	0.00	0.70
2	$S(\text{age} + \text{rain.winter})$	16	35,060.67	1.97	0.26
(h) Models testing for the effect of winter temperature					
1	$S(\text{age})$	15	35,058.70	0.00	0.54
2	$S(\text{age} + t_{\min}.\text{winter})$	16	35,060.61	1.91	0.21
3	$S(\text{age} + t_{\max}.\text{winter})$	16	35,060.73	2.03	0.20
(i) Models testing for the effect of days of air frost during winter					
1	$S(\text{age})$	15	35,058.70	0.00	0.62
2	$S(\text{age} + \text{af.winter})$	16	35,060.01	1.31	0.32
3	$S(\text{age} \times \text{af.winter})$	18	35,063.47	4.77	0.06
(j) Models testing for the effect of density					
1	$S(\text{age})$	15	35,058.70	0.00	0.51
2	$S(\text{age} + \text{density})$	16	35,060.50	1.80	0.21
3	$S(\text{age} + \text{density}_t)$	16	35,060.74	2.04	0.18
4	$S(\text{age} \times \text{density}_t)$	18	35,062.93	4.23	0.06
5	$S(\text{age} \times \text{density})$	18	35,063.47	4.77	0.05

We ran three sets of models (*a–c*), using the three top models for *p* and *r*; and *F* was fixed to its best model structure: additive effect of age, sex and period (Table 1). We tested for the effect of study period, year, sex, and age, and additive and interactive effects of these variables on *S*. We used the best base model for *S* (model 1; Table B3a) to test for the effects of (*d*) monthly rainfall, (*e*) monthly temperature, (*f*) monthly air frost, and (*g*) winter rainfall, (*h*) winter temperature, (*i*) winter air frost, and (*j*) index of population density. Best-supported models (Δ AICc < 5) for *S* are presented for each model set. Environmental covariates are: monthly mean daily maximum temperature (t_{\max}), monthly mean daily minimum temperature (t_{\min}), monthly total rainfall (*rain*), monthly days of air frost (*af*), density of breeding pairs (pairs/100 km²) in year *t* (*density*)

Nov November *Dec* December *Jan* January *Feb* February *Mar* March; for other abbreviations and table content descriptions, refer to Table 1

(Ratcliffe 1993), and substantially higher fidelity for juvenile peregrines during the population recovery period likely reflects relatively low population density during that period, and consequently, no shortage of territories locally, reducing the need for long-distance moves. This finding was further corroborated by the negative effect of population density on fidelity of juveniles during the recovery period when the peregrine population was increasing. As the population grew, territory occupancy became more saturated with fewer unoccupied sites; consequently, juveniles dispersed further from natal sites, leading to lower fidelity to the study area during the high-density phase. Dispersal distances of juveniles were greater, on average, in the most recent study period than in the earlier study period (Smith and McGrady, unpublished data). Taken together, these results provide evidence that dispersal in our study population was density dependent. Finally, we expected that fidelity rates would be lower for females than for males based on sexual differences in natal and breeding dispersal in peregrines and other raptors (Newton 1979; Mearns

and Newton 1984). The fact that in our current analysis, males showed less fidelity to the study area than females may be an artefact of the methodology, in which fidelity was assessed based not from distances moved, but from whether individuals were re-encountered inside or outside our extensive study area. Many birds made relatively long movements within this area, while others made short-distance movements from inside to outside. This measure of fidelity to area was required by the models, but may not necessarily accord with findings on dispersal based on actual distances moved.

The most parsimonious survival model provided evidence for age-specific differences in survival of peregrines. Consistent with findings of previous studies (Ratcliffe 1993; Kauffman et al. 2003; Craig et al. 2004), we found that survival was lower for juveniles than for older birds. Juveniles leave natal territories during their first summer (Newton 1979), so they presumably suffer higher mortality because of the risks of dispersal, their lack of hunting experience and their unfamiliarity with the new areas they

explore (Gonzalez et al. 1989). We found no evidence for differences in survival between subadults and adults. Even though subadults are less experienced and may face higher risks as a result, adults are more exposed to persecution during the nesting period (Newton 1979) and include some old birds that would be expected to have reduced survival prospects.

We had predicted that survival of juveniles would be lower during the high-density study period because in other species density-dependent effects tend to affect juveniles more than adults (Clutton-Brock et al. 1987; Newton 1998). Contrary to our expectations, survival rates for all age classes were slightly lower during the low-density than the high-density study period. This may have been due to the chronic, persistent effect of organochlorine pesticides during the earlier period. There is general agreement that poisoning by organochlorine contaminants was the primary cause of population decline of many raptors between 1947 and 1975, caused by a combination of reproductive failure and increased mortality. Despite a marked reduction in the use of organochlorines, some compounds were still being used well into the 1980s, and residues were still found in eggs (Nisbet 1988; Newton and Wyllie 1992). Due to their persistence and high fat solubility, organochlorines can accumulate in animal bodies, and pass from prey to predator, concentrating at successive steps in a food chain (Newton 1979). When the fat is metabolised, the residue shifts to other tissues and may cause reproductive failure or death depending upon the compound and level of poisoning.

Our finding that there was no evidence for density-dependent effects on survival rates suggests that peregrine survival in our primary study site was not substantially affected by population density, so that density-dependent effects were likely to be stronger on age of first reproduction. A direct consequence of higher density would be a shortage of territories, which can substantially affect age of first reproduction. For example, the age of first reproduction in our south Scotland—north England study area was substantially lower during the low-density study period (females, $2.90 \pm \text{SE } 0.59$ years; males, 3.58 ± 0.40 years) than the high-density study periods (females, 4.86 ± 0.66 years; males, 7.74 ± 1.27 years). Consequently, our results clearly demonstrate that density-dependent effects can influence demographic parameters differently and that such influences can vary across phases of population growth.

There was no evidence for sex-specific differences in survival, a finding also consistent with model-averaged estimates (Table A6, Online Resource). These results do not support our expectation that males, due to a smaller body size, would have lower survival than females. Our finding may not have been expected in a wholly undisturbed peregrine population because females are more likely than males to have been shot at nests as they incubate eggs and

brood chicks more than males. Among climatic variables, there was evidence that survival was positively affected by an increase in minimum monthly temperature in March. As expected, low winter temperatures tend to have negative effects on survival of endothermic organisms in cold environments (Angilletta et al. 2010), especially for inexperienced and mobile individuals, such as subadult raptors (Newton 1979). No other climatic variable examined affected peregrine survival.

Newton and Mearns (1988) reported peregrine survival rates for south Scotland during the 1980s that were based on the same data set we used in our study. Estimates of survival reported by Newton and Mearns (1988) were higher for adult breeders and lower for pre-breeders (juvenile and subadult combined) than those we found (Table A7, Online Resource). Differences between our estimates and those reported by Newton and Mearns (1988) likely reflect differences in methods used to estimate survival rates. For adult survival, Newton and Mearns (1988) used the proportion of birds handled at nest sites in one year that were re-caught at nest sites in a later year. Although this gave a minimum estimate of actual survival, it was still somewhat higher than the estimate for the later period obtained differently. We used Burnham's modelling framework (which can combine both mark-recapture and recovery data) to estimate survival, a method not developed when Newton and Mearns' (1988) results were published. In the present analyses, peregrines from both recapture and recovery >2 years old were classified as adults; these birds could have included younger birds that had not yet acquired territories, as well as older ones that may have been excluded from territories. Young floaters and senescent peregrines are likely to have lower survival than breeding adults, leading to a lower adult survival in the present study compared to the estimate of breeder survival reported by Mearns and Newton (1988).

To our knowledge, this study is the first to report rigorous estimates of true sex and age survival rates for peregrines in Europe (Table A7, Online Resource). Our estimate of juvenile survival is substantially higher than those reported from other parts of the peregrine's range, but estimates of adult survival are similar. Some of these differences might reflect differences in study design and estimation methods, but these differences may also be due to genuine differences in survival due perhaps to differences in habitat quality, food supply and migratory habits. On the other hand, our estimates of survival are within the range reported by previous studies that used mark-recapture or mark-recapture-recovery modelling frameworks to estimate survival (Table A7, Online Resource).

Burnham's (1993) modelling framework uses information on both live encounters and dead recoveries to estimate fidelity and true survival. Consequently, assumptions of both open population mark-recapture (live encounter)

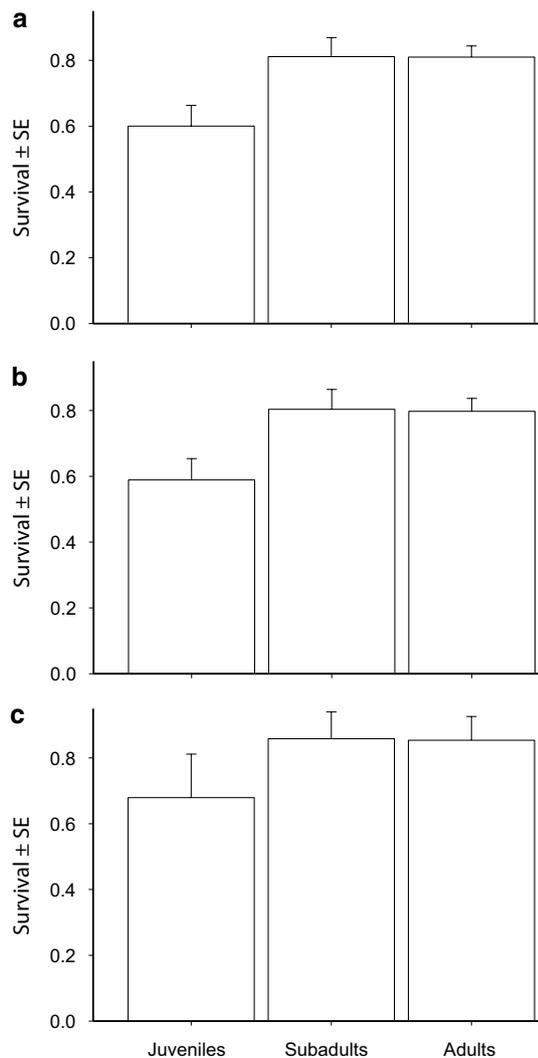


Fig. 3 Age-specific survival rates (\pm SE) of peregrines in south Scotland—north England: **a** overall annual estimates based on the most parsimonious model that included an effect of age on survival [model 1 (a); Table 2], **b** low-density study period (1974–1982) and **c** high-density study period (2002–2010) annual estimates based on the second best (and well-supported) model that included an additive effect of age and study period (model 2; Table 2). Age classes are: <1 year, juveniles; 1–2 years, subadults; and >2 years, adults

models and those required for tag recovery models apply to Burnham's model (Williams et al. 2002; Cooch and White 2014). These assumptions include: (1) homogeneity in capture and survival probabilities within an age class and/or sex, (2) homogeneity in recovery rates within an age class and/or sex, (3) independence of fates or encounter histories, (4) absence of tag loss, and (5) instantaneous sampling. While we have no reason to believe that assumptions inherent in mark-recapture models were violated, those specific to tag-recovery models are challenging to meet. This is in part because tag-recovery information generally depends

upon the willingness of the general public to report the identity of dead birds to the relevant authority. Consequently, recovery information is often limited and usually not unbiased, especially for some sex or age classes. Furthermore, to partition apparent survival into true survival (S) and fidelity (F), Burnham's model generally assumes that recovery of dead birds occurs outside of the area where peregrines were marked and recaptured. When mark-recapture and recovery area are the same, then F is estimated to be 1.0 because there is insufficient information to estimate permanent emigration. This, combined with small recovery sample sizes, likely explains high fidelity estimates for subadult peregrines in our study.

The primary mechanism underlying pesticide-related global decline in raptor populations appears to have varied geographically. In North America, reduction in reproductive success caused by DDT and related compounds (e.g. DDE) was considered to be the exclusive cause of population decline of peregrines and other raptors (Cade et al. 1988; Nisbet 1988; Peakall and Kiff 1988). However, reproductive failure attributable to DDT and related compounds was probably not the primary cause of population decline in British peregrines; instead, those declines coincided with the introduction of dieldrin, and adult mortality caused by that compound is believed to be the primary cause of raptor population declines in Britain at least until it was completely banned in 1986 (Ratcliffe 1970, 1993; Newton 1986). Our findings that survival of peregrines of all ages was somewhat lower during the earlier study period may indicate possible chronic effects of organochlorine pesticides, even though their use had been substantially reduced by that time. Because population growth rate of long-lived birds such as peregrines is proportionately more sensitive to changes in survival than reproductive rates (Wootton and Bell 1992; Stahl and Oli 2006; Krüger et al. 2010), even a small reduction in survival, particularly of adults, can drastically reduce population growth rate.

Author contribution statement MJM, IN and MKO conceived and designed the study. GDS, MJM, RM, IN and CR collected, and OEM, MKO and JAH analyzed, the data. MKO, GDS, OEM and MJM wrote the paper. All authors reviewed and edited the manuscript.

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