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RESEARCH ARTICLE

Reproductive performance of Peregrine falcons relative to the use of organochlorine pesticides, 1946–2021

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Abstract

1. Populations of some fish- and meat-eating birds suffered dramatic declines globally following the introduction of organochlorine pesticides during the late 1940s and 1950s. It has been hypothesised that these population declines during the 1950s–1970s were largely driven by a combination of reproductive failure due to eggshell-thinning, egg breakage and embryonic death attributable to DDT and its metabolites, and to enhanced mortality attributable to the more toxic cyclodiene compounds such as aldrin and dieldrin.
2. Using 75 years (1946–2021) of Peregrine falcon (*Falco peregrinus*) monitoring data (315 unique nest-sites monitored for 6110 nest-years), we studied the breeding performance of a resident Peregrine population in southern Scotland relative to the spatiotemporal pattern of organochlorine pesticide use.
3. We show that (i) Peregrine breeding success and measures of breeding performance increased substantially following the reduction in, and subsequently a complete ban on, the use of organochlorine pesticides; (ii) improvements in Peregrine breeding performance were more dramatic in southeastern Scotland where agriculture was the predominant land use than in southwestern Scotland where there was less arable and more forested land; (iii) Peregrines nesting closer to the coast generally had higher fledging success (that is, a higher proportion of clutches that produced at least one fledgeling) than those nesting inland farther away from the coast; (iv) low temperatures and excessive rain in May negatively affected Peregrine fledging success; and (v) Peregrine abundance increased in parallel with improvements in reproductive performance following the reduction and then complete ban on the use of organochlorine pesticides in the UK. However, recovery was gradual and occurred over four decades, and rate of recovery varied among measures of reproductive performance (egg, nestling and fledgeling production).

4. Our results suggest that the temporal pattern of organochlorine pesticide use strongly influenced Peregrine reproductive parameters but that the pattern of influence differed regionally. Overall results are consistent with the hypothesis that reproductive failure caused by organochlorine pesticides was an important driver of the decline in the south Scottish Peregrine population, and that improvements in all measures of breeding performance following a reduction and eventual ban on organochlorine use facilitated the observed increase in this population.

KEYWORDS
Brood size, clutch size, DDT, *Falco peregrinus*, fledging success, hatching success, long-term population monitoring, organochlorine pesticide

1 | INTRODUCTION

An important turning point in the history of conservation, and of conservation of raptorial birds in particular, followed the introduction and widespread use in agriculture of organochlorine pesticides such as DDT and the cyclodiene compounds, aldrin and dieldrin. Organochlorine pesticides are particularly detrimental to meat- and fish-eating birds because (i) these compounds are toxic and can cause direct mortality of adults or embryos; (ii) they are chemically stable so they can persist in the environment for decades; (iii) they are fat soluble and can bioaccumulate in bodies of birds and mammals; and (iv) they are capable of dispersing widely, far away from the location of their use, via natural processes or movement of individuals exposed to these compounds (Newton, 1979, 2017). HEOD, a metabolite of aldrin and dieldrin, is very toxic and negatively impacts raptor populations by causing direct mortality (Hudson et al., 1984; Newton, 1979, 1998; Prestt & Ratcliffe, 1972). On the other hand, DDT and DDE are much less toxic than HEOD, but also have devastating effects on raptor populations via a different mode of action (Newton, 1986, 1998, 2017). Even small quantities of DDE can induce eggshell thinning, egg breakage and death of embryos, thereby causing reproductive failure (Cooke, 1979; Newton, 1979, 1986, 1998; Ratcliffe, 1970).

Like many other raptorial birds, the Peregrine Falcon (*Falco peregrinus*; hereafter 'Peregrine') population in the UK suffered a dramatic population decline following the introduction of organochlorine pesticides during the 1940s–1950s (Newton et al., 1989; Newton & Wyllie, 1992; Ratcliffe, 1988, 1993). By 1963, the UK population had declined to approximately 44% of the level estimated for 1930–1939. Population declines were accompanied by territory desertion, small broods, egg-breaking, failure of intact eggs to hatch, and territories occupied by single birds only (Ratcliffe, 1988). High incidence of broken eggs in Peregrine eyries was observed across many locations in the UK during the 1950s, with no evidence of human or other outside interference (Ratcliffe, 1958). It was subsequently established that egg breakage and ensuing reproductive failure in Peregrines and other raptorial birds was a physiological consequence of eggshell thinning caused by DDE and death of embryos during incubation caused by DDT and dieldrin (Newton et al., 1999; Peakall, 1974, 1993; Peakall et al., 1976; Ratcliffe, 1967, 1970). Population declines of Peregrines and other raptorial birds in the UK and elsewhere were attributed to a combination of reduced hatching, hence breeding, success due to DDE and increased mortality due to aldrin/dieldrin (Newton, 1979, 1998, 2017; Prestt & Ratcliffe, 1972; Ratcliffe, 1993).

Whereas reproductive failure attributable to organochlorine pesticides has been suspected as a cause of the Scottish Peregrine population decline (Newton, 1979, 2017), reproductive success and measures of breeding performance of Scottish Peregrines have not been examined in detail relative to the use of organochlorine pesticides and their residues in the environment. Our goal was to assess the number of nesting pairs and different components of Peregrine breeding performance in relation to the presumed spatiotemporal pattern of organochlorine pesticide use in southern Scotland, using exceptionally long-term data (1946–2021). DDT was introduced for agricultural use in the UK in 1946–1947 and cyclodiene compounds in 1956, their use soon becoming widespread. Although the use of two cyclodiene compounds, aldrin and dieldrin, was progressively reduced during the 1970s (the use of dieldrin for sheep dipping was banned in 1966; Lockie et al., 1969), DDT was still being used until it was eventually banned in 1986 (Newton & Wyllie, 1992). We hypothesised that (1) Peregrine breeding performance would reach its lowest when organochlorine pesticides were most widely used, and highest after the residues of these compounds had largely diminished from the environment. Unfortunately, no data on the actual amounts of these pesticides used are available for anywhere in the United Kingdom. However, using chemical analysis of Peregrine eggs collected during 1963–1986, Newton et al. (1989) showed that the spatial pattern of the levels of DDE and HEOD in Peregrine eggs in the UK closely corresponded with the extent of agricultural land. Thus, we also hypothesised that (2) the negative effects of organochlorine pesticides on breeding performance would be stronger on Peregrines nesting in southeastern Scotland, because arable agriculture was the predominant land use there compared to southwestern Scotland where arable farming was less widespread and more land was forested, and that the rate of recovery in measures of breeding performance would differ between the two regions; (3) Peregrines nesting farther away from the coast would have lower breeding success than those nesting near the coastlines because the latter would also have access to coastal and marine birds that were likely to have been less exposed to organochlorine pesticides than birds nesting inland in more heavily farmed areas; and (4) Peregrine breeding success would also be negatively affected by excessive rain and low temperatures during the hatching period (April and May; see Mearns & Newton, 1988).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located in southern Scotland (Figure 1), a hilly region, coastal in the east and west rising inland to elevations of about 500–700 m. The region is characterised by mixed farming on the lower ground, with pasture and arable, and by open grassy sheepwalk, heather moor (*Calluna vulgaris*) and conifer plantations on the higher ground. During the study period, the biggest changes in habitats were related to forestry, including the planting and subsequent growth of forests in previously open hill areas, and the clear-cutting and re-planting of some longer-established forest areas. Peregrines were resident year-round and fed on a variety of avian prey, but racing and feral pigeons (*Columba livia*) were a particularly important source of food (Ratcliffe, 1993), at least until recent years when fewer became available (G. D. Smith, pers. obs.). In the west a greater proportion of land was forested than in the east where farming was more predominant. Owing to the higher elevation coupled with the influence of the sea and prevailing winds, the western part of the study area (arbitrarily set west of the M74 motorway, except for around Lanarkshire) was notably wetter and milder than the eastern part.

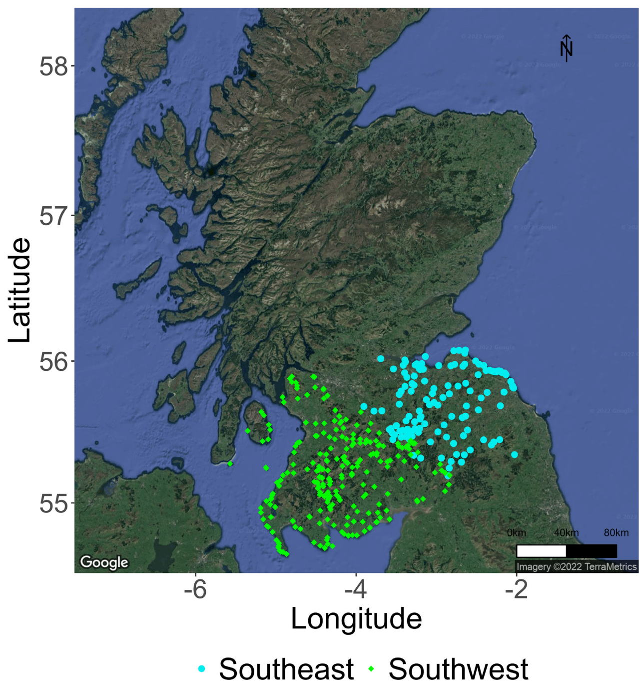

FIGURE 1 Location of Peregrine falcon nest sites monitored during this study in south Scotland, 1946–2021.

2.2 | Field methods

Every year since 1946, the Peregrine population in southern Scotland has been monitored by ornithologists, mainly experienced citizen scientists who, when it became necessary, operated under a government-issued Schedule 1 Licence (Nature Conservancy Council and Scottish Natural Heritage (now NatureScot) licence numbers 5644, 5443, 5600, 5644, 6560, 7788, 5648, 9423, 5426, 11250, and 12881; and British Trust for Orgnithology licence numbers 4255, and 8526). Field workers attempted to visit every known Peregrine site (crag or other terrain feature or building that could hold one or more Peregrine nest locations) 2–4 times during the nesting season to determine nest site occupancy, and if the nest site was occupied, an attempt was made to determine and record clutch size, brood size and the number of chicks that fledged from the nest. They also checked previously unoccupied locations that, because of their distance from active sites and availability of suitable habitat, might hold Peregrines. Generally, the first eggs were laid in late March–early April so that the first visits were made during March and April. At that time, it was often easy to determine, by the behaviour of the occupants, climbing to the nest ledge or viewing from a vantage point, whether a clutch had been started. At some inaccessible sites, the results of this first visit were inconclusive: birds could be recorded as present but further visits were required to determine breeding status.

If a site was occupied and eggs seemed to have been laid, an effort was made to determine final clutch size, providing this could be done without undue disturbance or revealing the site to potential onlookers. Sites that were not occupied in early visit(s) were visited later to check for late or missed occupancy. In addition, some coastal nest locations were inaccessible so for them clutch and brood sizes remained unknown, although the behaviour of adults (and sometimes later sightings of flying young) indicated whether young were reared. Nest sites with eggs were revisited when it was judged they would have chicks old enough to ring (ca. 2–5 weeks), mostly between 20 May and 20 June but sometimes extending to mid-July for late nesting pairs (Smith & McGrady, 2008). The number of young present at this stage was taken as the number fledging. Nevertheless, the majority, but not all, nests were also visited after fledging to check the number of flying young.

For each nest site, we recorded grid location, elevation, type of nesting habitat, type of nest site (active quarry, disused quarry, coastal cliff, inland cliff, small rocky outcrop, ravine, industrial or urban building).

2.3 | Covariates

Inclement weather during hatching or early chick stages can adversely affect nesting success (Mearns & Newton, 1988; Ratcliffe, 1993). We therefore compiled data on the following variables from UK Meteorological Office archives (Met Office, 2006): total monthly rainfall, total monthly number of rain days, and mean monthly minimum temperature in April and May. Weather data for southwestern Scotland were obtained from Eskdalemuir Weather Station (https://www.weatherhq.co.uk/weather-station/eskdalemuir); and for southeastern Scotland from Peebles Weather Station (https://www.metoffice.gov.uk/weather/forecast/gcvsx77db#?date=2022-05-25). Finally, we calculated the distance from each nest location to the nearest coastline using electronic versions of Ordinance Survey Maps. Values of climatic covariates are presented in Figures S1–S3.

2.4 | Data analysis and modelling

We analysed five variables related to Peregrine breeding success: clutch size (number of eggs per nest), brood size (number of young chicks per nest), number of fledglings (number of chicks that survived to ringing age, ~2–5 weeks), hatching success (proportion of nests with ≥1 eggs that hatched; also incorporates pre-ringing chick mortality), and fledging success (proportion of occupied nests with ≥1 eggs that fledged at least one chick). For the analysis of clutch or brood sizes, and the number of fledglings, we excluded all observations with incomplete egg or hatchling counts. Likewise, our analysis of the number of fledglings produced per nest was based only on observations with deemed complete fledgling counts (i.e. the number of chicks at ringing stage that were well developed and expected to fledge).

Data in the eastern and western portions of the study area were collected by different observers but using the same methodology, as described in Hardey et al. (2013). As well as dividing our data into eastern and western, we distinguished three periods relative to organochlorine pesticide use: (i) *Pesticide period* (until 1973; a period characterised by widespread and intensive use of organochlorine pesticides); (ii) *Recovery period* (1974–2002; a period characterised by a progressive reduction in organochlorine usage, followed by a complete ban in 1986). Owing to the persistence of organochlorine residues in the environment, we sought to quantify how long the effects of organochlorine pesticides were evident on Peregrine reproduction after the 1986 ban. The cut-off between the pesticide and recovery period (1974) was chosen because the effect of organochlorine pesticides on Peregrine reproductive parameters had been substantially reduced by the mid-1970s (Mearns & Newton, 1988); and (iii) *Stable period* (2002–2021), when the Peregrine population had recovered from the residual effects of organochlorines as evidenced by fairly stable number of breeding pairs (Smith et al., 2015).

All data (1946–2021) were used to calculate summary statistics, and to test for period-specific and regional differences. For each nest, we considered (1) a hatching attempt to be successful if ≥1 eggs hatched (hereafter, *hatching success*); and (2) a nesting attempt to be successful if ≥1 chicks reached at least the ringing stage (hereafter, *fledging success*). If a hatching or fledging attempt was successful, it was coded '1'; otherwise it was coded '0' for statistical analyses. We analysed hatching success, and fledging success and tested for the influence of region and period on the aforementioned measures of Peregrine reproduction using generalised linear mixed models (GLMM) with binomial distribution and logit-link (Agresti, 2015; Zuur et al., 2009). We used GLMMs with Poisson distribution and log-link for the analysis and modelling of the three breeding performance measures (clutch size, brood size and the number of fledglings per nest). We included the random effect of nest site in all analyses because almost all nest sites were sampled in two or more years.

We also tested for weather effects on fledging success using the monthly number of rain days, total monthly rainfall and mean minimum temperature in April and May of each year of the study, 1960–2021. Finally, we used 'distance to coast' to test the hypothesis that Peregrines nesting close to the coast would have higher reproductive success than those nesting inland farther from the coast. Testing included the singular effects of these factors, and additive and biologically meaningful interactive effects (2-way only) of these factors with the region (southeast and southwest) and study period relative to organochlorine use (pesticide, recovery and stable periods). Effects of covariates were assessed based on whether or not the addition of a covariate improved model parsimony. Covariate effects on nesting success were tested using the 1960–2021 subset of the data, because weather data were available only since 1960. All quantitative covariates were scaled to a mean of zero and a standard deviation of 1 to facilitate model convergence.

We used an information-theoretic approach using Akaike information criterion corrected for small sample size (AICc) for model selection statistical inference (Burnham & Anderson, 2002). All statistical analyses were performed in the R computing environment (Version 4.2.1; R Development Core Team, 2021). We used *lmer()* function in R package *lme4* to fit GLMMs (Bates et al., 2012). Model results were plotted using *plot_model()* function of *sjPlot* package for R (https://strengejacke.github.io/sjPlot/).

3 | RESULTS

3.1 | Non-laying by site-holding Peregrines

In this Scottish Peregrine population, a proportion of territories was occupied by territorial pairs or single birds that failed to produce eggs. During the pesticide period, apparent non-laying affected about 63% of all territories recorded as occupied in southeast Scotland and 38% of those in southwest Scotland (Figure S4). These estimated proportions dropped to about 30% in both southeast and southwest during the two later periods of recovery and stability. Occupancy of sites by non-breeding birds is difficult to record accurately, because it depends on one or two birds, or signs of their presence (faeces or prey remains), being evident at the time of a visit. Because of these uncertainties over site-holding but apparent non-laying Peregrines, we based the rest of our analyses only on pairs known to have laid one or more eggs, (but return to the question of non-laying pairs in the Discussion).

3.2 | Temporal pattern of Peregrine breeding success (1946–2021)

During 1946–2021, we monitored 315 nest sites (133 in southeastern and 182 in southwestern Scotland) that were occupied during ≥1 nesting seasons for a total of 6110 nest-years (1 nest site monitored for 1 year = 1 nest-year). The numbers of nest-years during the pesticide, recovery and stable periods were 411 (19 in southeast and 392 in southwest), 2599 (467 in southeast and 2132 in southwest) and 3100 (1189 in southeast and 1911 in southwest), respectively. Most commonly used nest sites were inland cliffs (34.7%), followed by coastal cliffs (23.8%) and small rocky outcrops (14.7%; $N = 5988$). During the pesticide period, nearly all nests were located either on inland cliffs and crags (70.8%) or on coastal cliffs and crags (12.4%, $N = 411$). The use of other, including urban, nest sites increased progressively over time concomitant with the increase in Peregrine abundance. The number of occupied nest sites monitored varied from four in 1946 and 1950 to 170 in 2007 (Figure 2a). The number of occupied nests monitored was ≥140 for all years since 1998 except in 2001 ($N = 55$) when travel restrictions imposed to control foot-and-mouth disease limited access to land, allowing us to visit only a fraction of the sites. Regionally, there were more occupied nest sites in southwestern than in southeastern Scotland, owing to longer coastline and more crags in the hills offering a greater number of potential nest sites (Figure 2a). Hatching and fledging success generally increased over time, but more so in southeastern than southwestern Scotland (Figure 2b,c). Interestingly, nearly all Peregrine reproductive parameters were initially lower, and improved later and faster, in southeastern Scotland than in southwestern Scotland (Figure 2b–f).

Clutch size, brood size and the number of fledglings per nest ranged from 1 to 5 (Figure 2d–f). However, the mean clutch size in southeastern Scotland (mean ± SE = 3.504 ± 0.025; $N = 806$) was substantially larger than the mean in southwestern Scotland (2.973 ± 0.024; $N = 1856$). Likewise, nests in southeastern Scotland fledged on average more chicks per successful nest (2.639 ± 0.031,

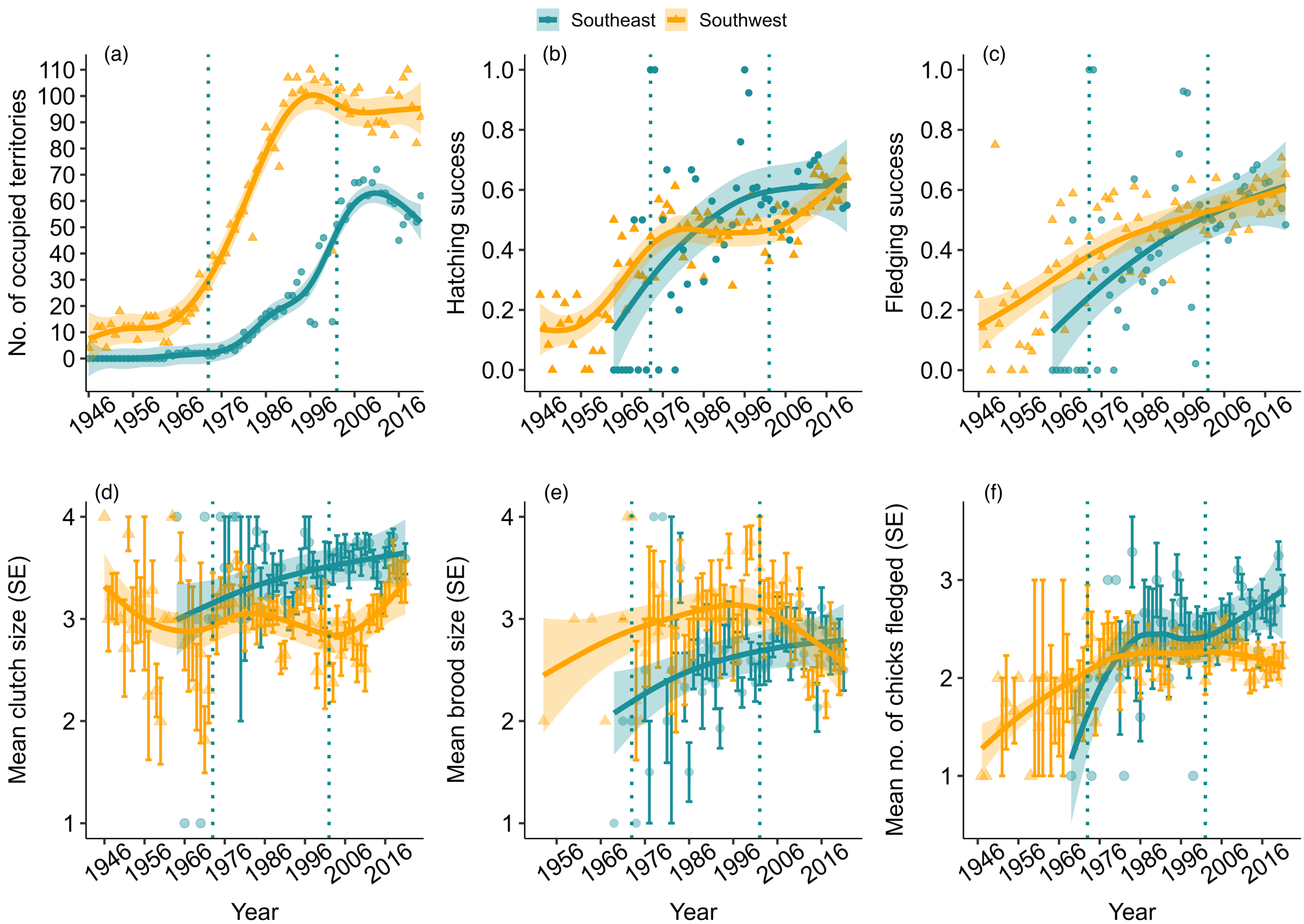

FIGURE 2 (a) The number of occupied territories; (b) hatching success, defined as the proportion of occupied nests with ≥1 hatchling; (c) fledging success, defined as the proportion of occupied nests that fledged ≥1 chicks during each year of study; (c) mean clutch size; (d) mean brood size, and (c) the mean number of chicks fledged per nest for each year of the study in southeastern and southwestern Scotland, 1946–2021. The low number of occupied territories in 2001 was an artefact of travel restrictions to control foot and mouth disease, which prevented access to many potentially occupied territories. The trendlines were fitted using R package *ggplot2* function *geom_smooth()* using generalised additive model (GAM) smoothing. Dashed vertical lines indicate demarcation between the pesticide and recovery period (1973), and between recovery and stable period (2002).

$N=846$) than those in southwestern Scotland (2.219±0.019, $N=2056$). However, initial brood sizes (brood size soon after hatching) in southeastern and southwestern Scotland were very similar (southeast: 2.689±0.033, $N=712$; southwest: 2.785±0.036, $N=609$). Measures of Peregrine breeding performance, especially the average number of chicks fledged per nest, increased over time but this increase was more pronounced in southeastern than in southwestern Scotland; these values eventually levelled off or reached levels similar to those in pre-pesticide times (Figure 2d–f).

3.3 | Regional differences and organochlorine pesticide effects (1946–2021)

Comparison of models designed to test for the regional and period-specific differences (Table 1) revealed that top models for fledging success included additive and interactive effects of region and period, suggesting that the temporal pattern of organochlorine pesticide use strongly influenced Peregrine reproductive parameters but that the pattern of influence differed regionally. However, the top

TABLE 1 Generalised linear mixed model comparison statistics testing for the effect of region (southeast and southwest Scotland), period relative to organochlorine pesticide use (pesticide, recovery and stable period), and both period and region on: (a) Hatching success, (b) Fledging success, (c) Clutch size; (d) Brood size and (e) Number of chicks fledged per successful nest, 1946–2021. (f) Model comparison statistics for top five models testing for the effect of climatic covariates.

Effect	*K*	AICc	ΔAICc	Weight
(a) Hatching success (1946–2021)				
Period	4	7783.629	0.000	0.439
Period + region	5	7784.335	0.706	0.308
Period × region	7	7784.736	1.107	0.252
Region	3	7902.578	118.949	0.000
Constant	2	7903.755	120.126	0.000
(b) Fledging success (1946–2021)				
Period × region	7	7974.370	0.000	0.931
Period + region	5	7980.923	6.554	0.035
Period	4	7981.007	6.637	0.034
Constant	2	8108.099	133.729	0.000
(c) Clutch size (1946–2021)				
Period + region	5	8831.336	0.000	0.627658
Period × region	7	8833.263	1.927	0.239461
Region	3	8834.441	3.105	0.132881
Period	4	8865.682	34.346	0.000
Constant	2	8865.682	45.235	0.000
(d) Brood size (1946–2021)				
Period + region	5	8831.336	0.000	0.628
Period + region	7	8833.263	1.927	0.239
Region	3	8834.441	3.105	0.133
Period	4	8865.682	34.346	0.000
Constant	2	8876.571	45.235	0.000
(e) Number of chicks fledged (1946–2021)				
Period × region	7	7974.370	0.000	0.931
Period + region	5	7980.923	6.554	0.035
Period	4	7981.007	6.637	0.034
Constant	2	8108.099	133.729	0.000
Region	3	8109.922	135.553	0.000
(f) Effect of weather covariates on fledgling success (1960–2021)				
Period × region + may_min_temp	8	7562.798	0.000	0.754
Period × region + may_tot_rainfall	8	7565.958	3.160	0.155
Period × may_min_temp	7	7568.593	5.796	0.042
Period + region × may_tot_rainfall	7	7570.583	7.786	0.015
Period × may_min_temp	5	7571.720	8.922	0.009

Note: Covariates are: may_min_temp = minimum temperature in May; and may_tot_rainfall = total rainfall in May (for a comprehensive model selection table, see Table S2). A '+' indicates additive effect, whereas '×' indicates both additive and interactive effects of the covariates.

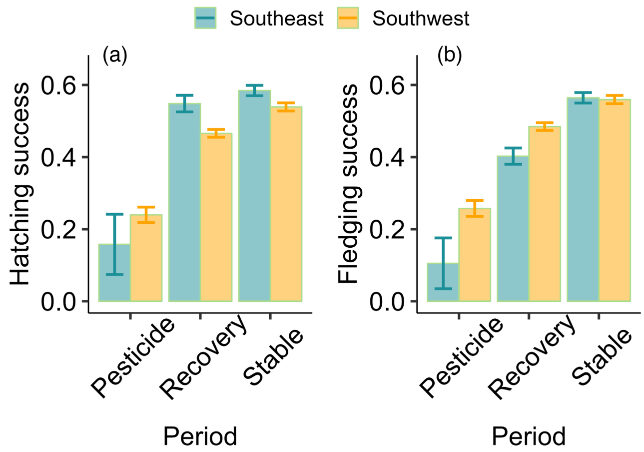

FIGURE 3 Probability of successful hatching (a) and fledging (b) by periods relative to pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) and region (southeast and southwest Scotland), 1946–2021.

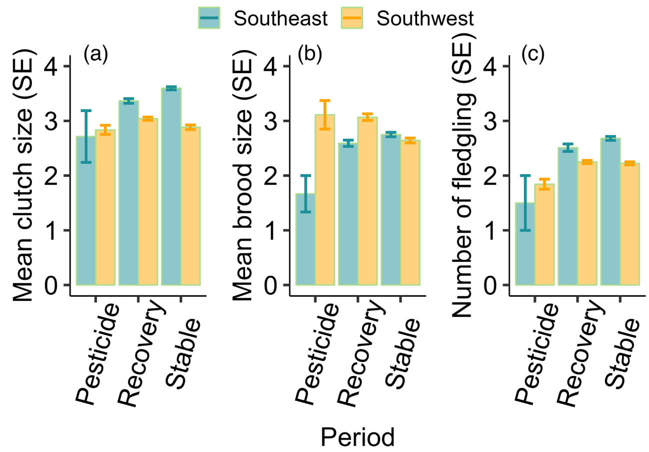

FIGURE 4 Mean (±SE) clutch size (a), initial brood size (b) and number of fledglings (c) by periods relative to organochlorine pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) and region (southeast and southwest Scotland), 1946–2021.

model for hatching success included an effect of period only, suggesting strong evidence for the influence of period but little or no evidence for regional differences in hatching success. In southeastern Scotland, hatching success ranged from a low of 0.158 ± 0.084 during the pesticide period to 0.585 ± 0.014 during the recovery period; while equivalent figures for fledging success were 0.105 ± 0.023 and 0.564 ± 0.014, respectively (Figure 3a,b). In southwestern Scotland, hatching success ranged from 0.359 ± 0.035 during the pesticide period to 0.539 ± 0.011 during the recovery period; and fledging success from 0.375 ± 0.035 to 0.560 ± 0.011 (Figure 3a,b; Table S4).

Nearly all measures of breeding performance also varied across periods and regions (Table 1). In southeastern Scotland, clutch size, brood size and the number of fledglings per successful nest increased from 2.714 ± 0.474 to 3.596 ± 0.003, 1.667 ± 0.333 to 2.751 ± 0.041, and 1.500 ± 0.50 to 2.680 ± 0.035 during the pesticide period and stable period, respectively. The difference in measures of breeding performance between the pesticide and recovery periods were modest in southwestern Scotland (Figure 4a–c; Table S4).

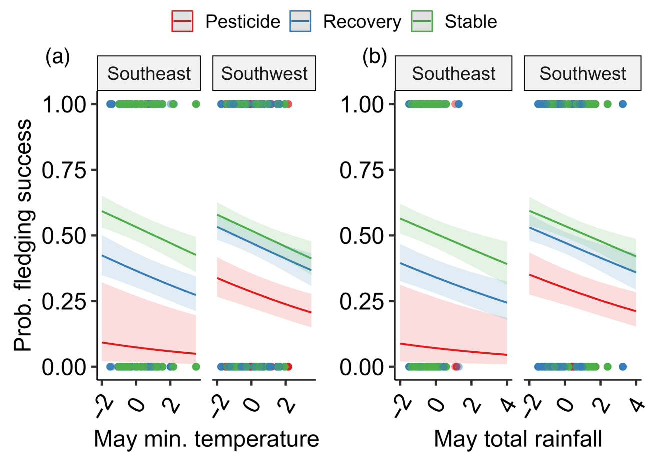

FIGURE 5 The influence of total rainfall (a) and mean minimum temperature (b) in May on Peregrine fledging success for each period relative to presumed levels of organochlorine pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) in southeast and southwest Scotland, 1960–2021. Temperature and rainfall data were scaled to mean of zero and standard deviation of 1.0 to facilitate model convergence. Filled circles indicate observed fledging success (1 = fledged ≥1 chicks; 0 = no chicks fledged).

3.4 | Factors influencing Peregrine fledging success (1960–2021)

The most parsimonious model testing for covariate effects revealed that Peregrine fledging success was strongly affected by minimum temperature and total rainfall in May. The top two models included additive and interactive effects of region and period, and an additive effect of May minimum temperature and May total rainfall, respectively (Table S2). In fact, all top models (cumulative AIC weight ≥ 0.99) included the effect of these two covariates. Both minimum temperature and total rainfall in May negatively influenced Peregrine fledging success in both regions and across all periods (Figure 5a,b). There was strong evidence for a negative effect of distance to coast (ΔAICc comparing *period × region* model with *period × region + distance to coast* = 208.12; $\beta \pm SE = -0.12174 \pm 0.05$; Figure S5). However, this model was much less supported compared to other models in the candidate model set (Table S2).

4 | DISCUSSION

After the nationwide decline of Peregrines in the UK, relatively few (≤21) territories were known to be occupied in south Scotland until 1970 (Figure 2a), which along with large values of mean nearest-neighbour distance (Figure 6), suggested that the Peregrine population in that region was small (in line with the depressed number of breeding Peregrines at that time worldwide,

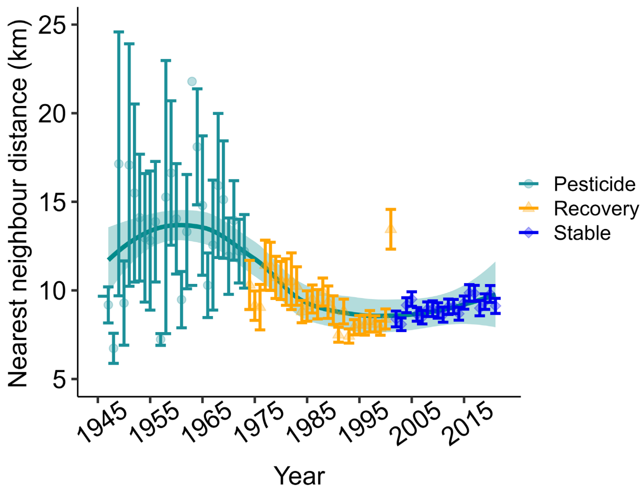

FIGURE 6 Mean nearest-neighbour distance among nest sites for each year of the study in southern Scotland, 1946–2021. Periods relative to organochlorine pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) are identified by different colours.

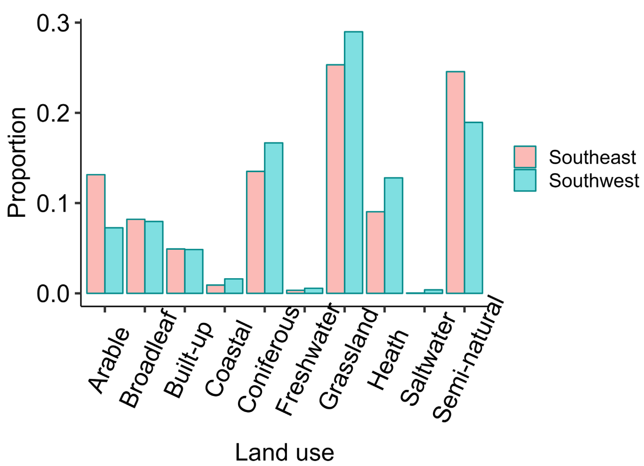

FIGURE 7 The proportion of land in different land use categories in southeast and southwest Scotland. Land use categories are: arable = arable land; broadleaf = broadleaf woodland; built-up = built-up areas; coastal = coastal areas; coniferous = coniferous woodland; freshwater = freshwater; grassland = improved grassland; heath = mountain, heath and bog; saltwater = saltwater; semi-natural = semi-natural grassland. Data from Morton et al. (2020).

Cade et al., 1988; Cade & Burnham, 2003). Subsequently, the population increased steadily for about 20 years, then more or less stabilised (McGrady et al., 2017; Smith et al., 2015). The increase in Peregrine abundance during the recovery period was accompanied by improvements in virtually all measures of reproductive performance albeit at different rates: hatching and fledging success (Figure 2b,c), as well as clutch size, initial brood size and the number of chicks fledged per nest (Figure 2d–f). Over the whole study period, improvements in measures of reproductive success were later but much more pronounced in southeastern Scotland, where the proportion of arable land is nearly twice as great (Figure 7; Figure S6).

In southeastern Scotland, only about 37% of the occupied territories were known to produce eggs during the pesticide period compared with about 70% during the recovery and stable periods. The increase in the proportion of occupied territories that produced eggs in southwest was modest, ranging from 61% during the pesticide period to about 70% during the recovery and stable periods (Figure S4). The relatively high proportion of apparent non-laying but site-holding birds during the pesticide period (especially in southeast) could have been due in part to the laying and instant breakage of eggs rather than to actual non-laying. These uncertainties mean that the impact of organochlorine pesticides on Peregrine breeding may have been greater than the remaining data presented here suggest, especially in southeastern Scotland.

4.1 | Time trends in reproduction

During the early part of the study, Peregrines in southwestern Scotland experienced higher hatching and fledging success, and also produced and fledged larger broods than those nesting in southeastern Scotland. Measures of Peregrine reproductive performance started improving as the use of organochlorine pesticides was progressively reduced; however, this improvement occurred later and at a faster rate in southeastern Scotland. The recovery occurred gradually over four decades, and the rate of recovery differed among measures of breeding performance (Figure 2b–f). We performed detailed analysis of the various measures of reproductive performance in relation to three periods of pesticide use, population recovery and population stability, respectively. Consistent with our expectations, we found that hatching and fledging success were lowest during the pesticide period and highest during the stable period when effects of organochlorine pesticides had disappeared (Figures 3 and 4). These period-specific differences were much greater in southeastern Scotland where arable agriculture was (and remains) the predominant land use, and organochlorine pesticide use was likely to have been greater (Newton et al., 1989; Newton & Wyllie, 1992) than in the mainly pastoral and forested southwestern Scotland (Figure 7). In southeastern Scotland Peregrine territories were 9.7 times more likely to experience hatching success, and 13.1 times more likely to experience fledging success during the stable period than during the earlier pesticide period. In southwestern Scotland, changes across periods in measures of breeding performance were also substantial, but not as great as in southeastern Scotland (Figures 3 and 4).

This regional difference in degree of change over the study period (Figure 2) suggests that southeastern Peregrines may have been more strongly influenced by organochlorine pesticides than those in the southwestern Scotland. This would have been expected because of the greater predominance of arable land in the southeast (Figure 7; Figure S6) and the likely greater use of organochlorine pesticides and their transfer to Peregrine prey species, and thence to Peregrines. As the use of organochlorine pesticides diminished, measures of Peregrine reproductive success improved and, in both regions, stabilised during the 1990s (Newton et al., 1989). High levels of polychlorinated biphenyls (PCBs) were also detected in Peregrine eggs from Southern Scotland during the 1970s–1980s, especially in those from coastal regions, but there was no evidence that, at the levels found, PCBs negatively affected Peregrine reproductive success (Newton et al., 1989).

The rapid improvement in hatching success and more gradual but continuous improvement in fledging success, and the regional differences in the timing of improvements, suggest that organochlorine pesticides contributed to Peregrine population decline at least partly by causing nesting attempts to fail. Also, positive changes in measures of reproductive success, probably resulting from the declines of those pesticides in the general environment, allowed Peregrine numbers to increase in south Scotland (Newton, 1979; Newton et al., 1989; Newton & Wyllie, 1992). It is impossible for us to say whether adult survival also improved over the study period, but by the 1970s, when the first study of annual adult survival was made, it had already reached >90% (Mearns & Newton, 1984), which is high compared to other raptors of similar size (Newton et al., 2016).

4.2 | Regional differences

By the 1990s, all measures of reproductive success in southeastern Scotland had recovered to similar levels as those in southwestern Scotland. Interestingly, while brood size and the number of fledglings per nest increased consistently until recently in southeastern nests, in the southwest measures of Peregrine reproductive success started declining during the mid-1990s. The timing of these declines coincided with changes in pigeon racing routes. Previously, racing pigeons were flying north–south (and vice versa) predominantly on the west side of Britain; but in more recent years pigeon racing routes were shifted to the east side (G. D. Smith, C. J. Rollie & R. Mearns, pers. obs.). Domestic and feral pigeons are a preferred prey for British Peregrines, accounting for >50% of diet by biomass in some areas, including southern Scotland (Dixon & Drewitt, 2018; Mearns, 1983; Ratcliffe, 1993). This change in racing routes is likely to have reduced the availability of pigeons in the southwest and accounted for the reduction in Peregrine reproductive success, especially the number of fledglings there, and possibly raised their abundance in the southeast.

In addition to the change in pigeon abundance, the soils in southeastern Scotland are generally more fertile than those in southwest Scotland, habitats are more productive, potential prey more abundant and the weather dryer. For these reasons, too, once organochlorine use had ceased, we expected Peregrine nests in southeastern Scotland to be more successful and productive than those in the southwest. During the pesticide period, southwestern nests were ~2 times more likely to experience hatching success (15.8% in southeast vs. 35.9% in southwest) and ~3.5 times more likely to fledge chicks (10.5% in southeast vs. 37.5% in southwest) than southeastern nests. During this period, southwestern nests also produced larger broods (1.67 in southeast vs. 3.29 in the southwest) and fledged more chicks per nest (1.5 in southeast vs. 1.90 in southwest). However, once the direct and residual effects of organochlorines disappeared, southeastern nests experienced similar or marginally better hatching success (58.5% in southeast vs. 53.9% in southwest) and fledging success (56.5% in southeast vs. 56.0% in southwest). On average, they also produced larger clutches (3.6 in southeast vs. 2.9 in southwest) and fledged more chicks per nesting attempt (2.7 in southeast vs. 2.2 in southwest; Table S1).

4.3 | Influence of weather and seacoast

Excessive rain and cold during hatching or early hatchling stage can negatively impact Peregrine breeding success (Mearns & Newton, 1988). Consistently, we found that minimum temperature and total rainfall in May strongly negatively affected Peregrine fledging success in our study area (Table 1f; Figure 5a,b). No other weather variables considered in our study had discernible effects on Peregrine reproductive success.

Because Peregrines in coastal areas have access to both terrestrial, and coastal/marine prey, they probably had a greater, as well as less contaminated, food-supply (Mearns & Newton, 1988). Correspondingly, we found that nests closer to the coast produced more young, especially during the pesticide period in southeastern Scotland (Figure S5).

4.4 | Comparison with previous studies in the same region

Our estimates of clutch size and brood size for the recovery period are similar to those reported by Mearns and Newton (1988) based on data collected in southwest Scotland during 1974–1982. However, our estimates of the number of fledglings per nest for the recovery (2.2–2.5) and stable periods (2.2–2.7; Table S1) were substantially greater than those reported by Mearns & Newton (1.06–1.26 per breeding pair). These differences suggest that Peregrine breeding success may have further improved between 1974 and 1982 (when organochlorine pesticides were present in reduced levels and declining), and at the end of the recovery period and into the stable period (midway through recovery, 1990–present). Also, Peregrines in Mearns and Newton's study nested almost exclusively on natural cliffs, whereas only about half (47.9%) of the nests in the present study (1946–2021) were on cliffs. Despite the increase in non-cliff nest sites, cliffs were clearly the preferred sites, which were more consistently occupied and generally more successful in fledging young (McGrady et al., 2017). The use of other nest types (e.g. quarries, urban and industrial sites, and small rocky outcrops) increased as Peregrine abundance rose and cliff-sites became ever more limited.

4.5 | Comparison with trends elsewhere

The trajectory of the Peregrine population in our study area was one of decline during the organochlorine pesticide era followed by slow recovery starting in the mid-1970s, after the use of these contaminants was substantially reduced, and subsequently, banned (Ratcliffe, 1988, 1993). The recovery gathered momentum and trended upward through the 1980s. By the mid- 1990s recovery was effectively complete. In Britain as a whole, minor variations from the overall upward trend occurred in some regions and may have been linked to other factors such as persecution and reduced food availability, notably racing pigeons (Banks et al., 2010). Studies in other parts of the world that covered a similar time period suggest a similar pattern of decline, recovery and stability as observed in south Scotland (e.g. Norway: Nygård et al., 2019; Denmark: Andreasen et al., 2018; Hungary: Bagyura et al., 2009; circumpolar region: Franke et al., 2020; Jura Mountains in France and Switzerland: Monneret, 2009, Monneret et al., 2022; Australia: Olsen et al., 1992; various regions in North America: Cade & Burnham, 2003, Enderson et al., 1995). In our study area, the overall recovery of the Peregrine population was underpinned by gradual and spatially asynchronous improvement in all measures of reproduction, including clutch size, hatching success, brood size and fledging success over time. Because our study started when organochlorine pesticides were being introduced to the UK, we were able to document how reproductive parameters were affected by the extensive agricultural use of organochlorines, and show how they changed as the use of organochlorines was progressively reduced and ultimately banned (Figure 2a–f). Furthermore, we show that the rate of recovery occurred later and at a faster rate in southeastern Scotland where Peregrine reproduction was more severely curtailed due to extensive agricultural use of organochlorines, compared to primarily pastoral and forested southwestern Scotland (Figure 7). Unfortunately, no comparable data based on continuous monitoring of Peregrine population trend and breeding success from the pesticide period to recent years are available; thus, it is difficult to say if the improvements in Peregrine reproductive parameters and the rate of population recovery in our study area is similar to those observed in other Peregrine populations.

4.6 | The conservation value of monitoring raptor populations

Novel contaminants with detrimental effects on wildlife continue to be introduced into the environment (Cuthbert et al., 2011; Oaks et al., 2004) and other anthropogenic activities such as persecution occur in some regions (Amar et al., 2012; Newton, 2021). Indeed, the Scottish Peregrine population has declined in recent decades, in some locations by ≥20%, most likely due to human persecution, as illegal killing and destruction of eggs are still prevalent on moorland managed for Red Grouse (Amar et al., 2012; Newton, 2021; Wilson et al., 2018; also see Figure 2a). More widely, for Britain as a whole, Robinson and Wilson (2021) reported a recent decline in the survival of juvenile Peregrines, and hypothesised mortality due to illegal persecution as a possible cause. Only if this residual persecution can be stopped is the Peregrine population likely to fully recover throughout the British range. Similar recent declines in Peregrine abundance and reproductive output have been reported from Jura Mountains in France and Switzerland, although the causes of these declines are not well understood (Kéry et al., 2022). The involvement of recently introduced contaminants cannot be ruled out as a possible cause of recent declines in Peregrine abundance and reproductive output in some areas.

The main goal of our study was to provide a thorough assessment of Peregrine reproductive parameters using exceptionally long-term monitoring data. These data provide strong support to the hypothesis that Peregrine population declines during the 1950–1970s were largely driven by poor reproductive performance attributable to widespread use of organochlorine pesticides in the study region, and show that Peregrines responded positively to the reduction and subsequent ban on the use of these chemicals. Although comparable data are not available from other Peregrine populations over such a long period, we expect that similar demographic mechanisms underlie the recovery of Peregrine populations in other parts of the world where organochlorine effects were a main cause of population declines (Banks et al., 2010; Nygård et al., 2019; Olsen et al., 1992; Ratcliffe, 1993; Wilson et al., 2018). Nevertheless, residual effects remain in some countries (García-Fernández et al., 2008; Weber et al., 2003), and over the last two decades organochlorines were still in use in parts of the southern hemisphere (Abbasi et al., 2016; Aver et al., 2020; Martínez-Lopez et al., 2015; Smith & Bouwman, 2000). Peregrines and other raptors have clearly played a prominent role in highlighting the ecological devastation caused by organochlorine pesticides (Baril et al., 2015; García-Fernández et al., 2008; Newton, 1979; Newton et al., 1989; Ratcliffe, 1958, 1967), and the continued monitoring of their populations could in future reveal impacts of other contaminants, enabling remedial action to be taken in a timely manner.

AUTHOR CONTRIBUTIONS

Madan K. Oli, Michael J. McGrady, George D. Smith, Ian Newton and Xavier Lambin conceived the ideas and led the writing of the manuscript. George D. Smith, Michael J. McGrady, Ian Newton, Chris J. Rollie and Richard Mearns designed the field study and collected data. Madan K. Oli, Vratika Chaudhary and Xavier Lambin performed data analyses with the help of all authors. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the University of Florida Institutional Repository: https://original-ufdc.uflib.ufl.edu/l/IR00012126/00001 (Oli et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. The mean clutch size (A), brood size (B), and number of fledglings per nest during each period relative to organochlorine pesticide use (period) and region of the study (southeastern and southwestern Scotland), 1946–2021. Standard error (SE) lower and upper 95% confidence limits (LCL and UCL, respectively), sample size (N) and range of values are also given.

Table S2. Generalized linear mixed model comparison statistics testing for the effect of covariates on Peregrine fledging success. Covariates are: region = southeast and southwest Scotland; period = period relative to organochlorine pesticide use (pesticide, recovery and stable period); may_min_temp = minimum temperature in May; may_tot_rainfall = total rainfall in May; may_tot_raindays = total number of rain days in May; april_tot_rainfall = total rainfall in April; april_tot_raindays = total number of rain days in April; and dist_to_coast_km = distance to coastline in kilometers. The number of parameters (K), Akaike Information Criterion corrected for small sample size (AICc); difference in AICc (ΔAICc) and model weight (Weight) are presented. A '+' indicates additive effect, whereas '*' indicates both additive and interactive effects of the covariates.

Figure S1. (A) Histogram of elevation (meters above sea level) of Peregrine nest sites in southeast and southwest Scotland, 1946–2021. (B) Histogram of distance from Peregrine nest sites to the nearest coastline in southeast and southwest Scotland, 1946–2021.

Figure S2. (A) Total number of rain days (raindays) in April and May; (B) Total monthly rainfall in April and May in southeast and southwest Scotland for each year of study, 1960–2021. Weather data for southwestern Scotland were obtained from Eskdalemuir Weather Station (https://www.weatherhq.co.uk/weather-station/eskdalemuir); for southeastern Scotland, weather data were obtained from Peeble Weather Station (https://www.metoffice.gov.uk/weather/forecast/gcvsx77db#?date=2022-05-25).

Figure S3. Mean minimum temperature (oC) in April and May in southeast and southwest Scotland for each year of study, 1960–2021. Temperature data for southwestern Scotland were obtained from Eskdalemuir Weather Station (https://www.weatherhq.co.uk/weather-station/eskdalemuir); for southeastern Scotland, weather data were obtained from Peebles Weather Station (https://www.metoffice.gov.uk/weather/forecast/gcvsx77db#?date=2022-05-25).

Figure S4. The proportion of occupied territories that produced ≥1 eggs (laying success) by periods relative to pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) in southeast and southwest Scotland, 1946–2021.

Figure S5. The influence of distance to coastline on fledging success for each period relative to organochlorine pesticide use (Pesticide: ≤1973; Recovery: 1974–2002; and Stable: 2003–2021) in southeast and southwest Scotland, 1960–2021. Distance data were scaled to mean of zero and standard deviation of 1.0 to facilitate model convergence.

Figure S6. The proportion of different land cover types in south Scotland based on the UK Center for Ecology and Hydrology (UKCEH) Land Cover Map 2019 (Morton et al., 2019). This land cover classification scheme characterizes the land cover of Great Britain according to the UK Biodiversity Action Plan (https://hub.jncc.gov.uk/assets/2728792c-c8c6-4b8c-9ccd-a908cb0f1432), and offers a comprehensive and standardized framework for categorizing and analyzing land cover across Britain.

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