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Territory occupancy and breeding success of Peregrine Falcons *Falco peregrinus* at various stages of population recovery

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Organochlorine pesticides disrupted reproduction and killed many raptorial birds, and contributed to population declines during the 1940s to 1970s. We sought to discern whether and to what extent territory occupancy and breeding success changed from the pesticide era to recent years in a resident population of Peregrine Falcons *Falco peregrinus* in southern Scotland using long-term (1964–2015) field data and multi-state, multi-season occupancy models. Peregrine territories that were occupied with successful reproduction in one year were much more likely to be occupied and experience reproductive success in the following year, compared with those that were unoccupied or occupied by unsuccessful breeders in the previous year. Probability of territory occupancy differed between territories in the eastern and western parts of the study area, and varied over time. The probability of occupancy of territories that were unoccupied and those that were occupied with successful reproduction during the previous breeding season generally increased over time, whereas the probability of occupancy of territories that were occupied after failed reproduction decreased. The probability of reproductive success (conditional on occupancy) in territories that were occupied during the previous breeding season increased over time. Specifically, for territories that had been successful in the previous year, the probability of occupancy as well as reproductive success increased steadily over time; these probabilities were substantially higher in recent years than earlier, when the population was still exposed to direct or residual effects of organochlorine pesticides. These results are consistent with the hypothesis that progressive reduction, followed by a complete ban, in the use of organochlorine pesticides improved reproductive success of Peregrines in southern Scotland. Differences in the temporal pattern of probability of reproductive success between south-eastern and south-western Scotland suggest that the effect of organochlorine pesticides on Peregrine reproductive success and/or the recovery from pesticide effects varied geographically and was possibly affected by other factors such as persecution.

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INTRODUCTION

Soon after the publication of Ratcliffe's (1967) seminal paper, it became evident that egg breakage and ensuing reproductive failure in some raptorial species were widespread, and nearly global in extent. Subsequent studies demonstrated that this was a consequence of eggshell thinning caused by dichloro-diphenyl-dichloroethylene (DDE, a dichloro-diphenyl-trichloroethane (DDT) derivative) (e.g. Peakall 1970, Peakall *et al.* 1976), and death of embryos during incubation caused by organochlorines such as DDT and dieldrin (Heath *et al.* 1969, Porter & Wiemeyer 1969, Enderson & Berger 1970). It is now well established that DDE contributed substantially to raptor population declines observed during the 1950s to 1970s by causing the thinning of eggshells, thereby decreasing both clutch size and egg viability (Ratcliffe 1970, 1993, Cooke 1979, Newton 1974, 1979).

DDE residues, eggshell thinning, reproductive failure and associated population declines were reported from across the geographical range of Peregrines *Falco peregrinus*, and global population declines were primarily attributed to DDT, although mortality of adults due to cyclodiene compounds and persecution by humans also played important roles in population declines in Britain and elsewhere (e.g. Ratcliffe 1970, 1993, Newton 1979, 1998, Nisbet 1988, Enderson & Berger 1970). The use of organochlorines was progressively reduced in Britain, and more or less completely banned from 1986. Concomitantly, organochlorine residues in raptor tissues declined and Peregrine populations began to recover (Newton 1979, Cade *et al.* 1988, Newton & Mearns 1988, Newton *et al.* 1989, Banks *et al.* 2010). The British population was thought to have fully recovered and reached a level higher than in the pre-pesticide era by the early 2000s (Crick & Ratcliffe 1995, Banks *et al.* 2010, Smith *et al.* 2016).

Despite wide recognition of the disruption of reproduction in many raptorial birds caused by organochlorine pesticides, the temporal pattern and mechanisms underlying changes in Peregrine breeding success from the 1960s (when organochlorine pesticides were still in use) to recent years (when the population is believed to have largely recovered and reached a presumed equilibrium density in most areas; Smith *et al.* 2015) remain poorly understood. Because we lacked data on the temporal and spatial pattern on the use of organochlorine pesticides in the UK, it was not possible to test directly for the effect of these compounds on the Peregrine population. If organochlorine pesticides had indeed adversely influenced reproductive success and survival in our study population (as the data on DDE and eggshell thinning suggested), it seems reasonable to expect that progressive reduction followed by a complete banning of the use of these compounds should be reflected in the temporal pattern in territory occupancy and breeding success. To test this idea, we applied multi-state, multi-season occupancy models (MacKenzie *et al.* 2009, 2010, Martin *et al.* 2009, Bailey *et al.* 2014) to long-term (1964–2015) data on Peregrine territory occupancy and productivity in southern Scotland. Specifically, we predicted an increase in probability of occupancy over time as the population recovered from pesticide-related declines, and an increase in the probability of successful reproduction as the severity of reproductive failure attributable to DDT residues decreased following the complete banning of organocholorine pesticides in 1986. Because Peregrines nesting in habitats actively managed for hunting Red Grouse *Lagopus lagopus scotica* generally experience increased persecution (Amar *et al.* 2012), we also predicted a lower reproductive success among Peregrines nesting in areas managed for grouse than those nesting in habitats that were not. Finally, because high density would mean more birds are available to occupy vacant territories, we predicted a positive effect of population density (or a density index) on occupancy probability.

METHODS

Study areas

The study area is located in southern Scotland (Fig. 1). The landscape is hilly, coastal in the east and west rising inland to elevations of about 500–700 m. This region is characterized by mixed farming in the lower ground, with pasture and arable land, and by open grassy sheepwalk, Heather *Calluna vulgaris* moor and conifer plantations on

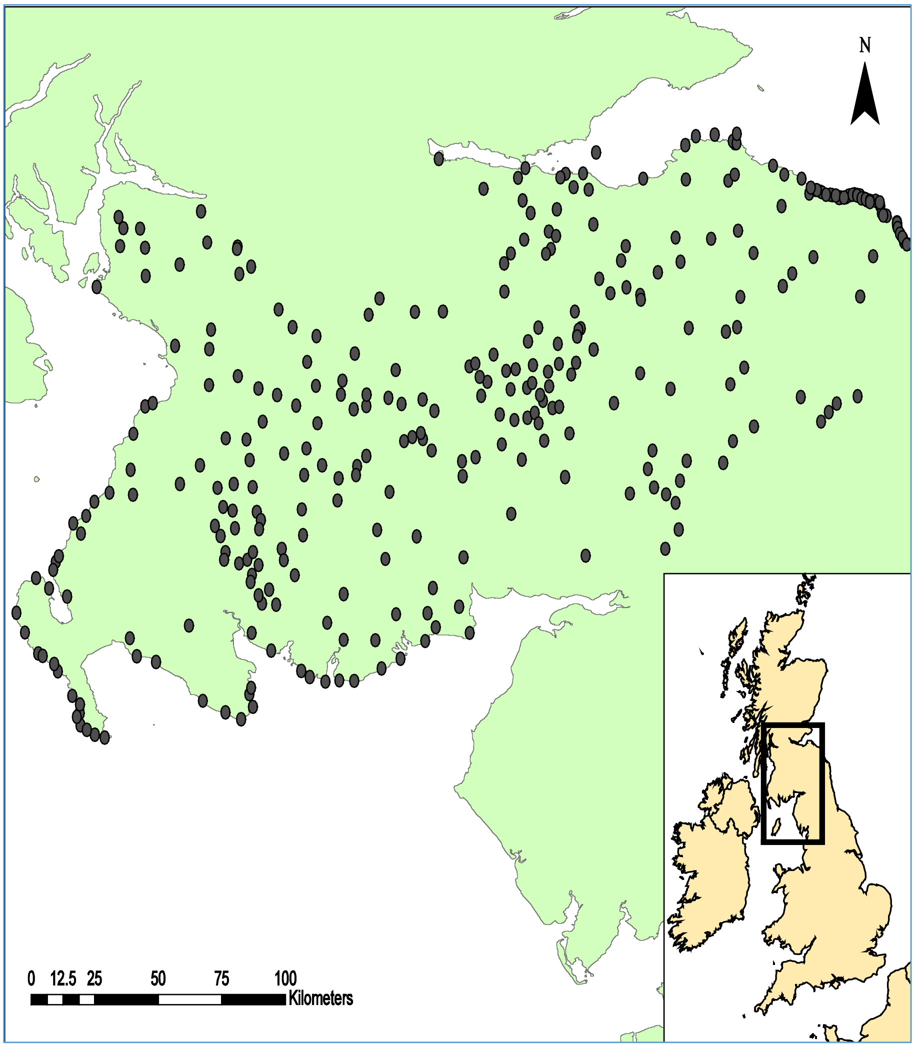

Figure 1. Southern Scotland study area, showing the location of Peregrine Falcon territories, 1964–2015. [Colour figure can be viewed at http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X]

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 areas, and the clearcutting of some mature areas. Peregrines are resident and feed on a variety of avian prey, but racing and feral pigeons *Columba livia* are a particularly important source of food (Ratcliffe 1993), although their importance may be changing. There is no clear boundary between the eastern and western parts of the study area, but in the west, proportionally more arable land is coastal and more land is forested than in the east. There is also proportionally more land managed for Red Grouse shooting in the west. Additionally, due to the higher elevation coupled with the influence of the sea and prevailing winds, the western part of the study area is notably wetter and milder than the eastern part.

Field methods

Every year since 1946, the Peregrine population in our southern Scotland study area has been monitored, mainly by experienced volunteer citizen scientists. However, data were sparse until the mid-1960s, so our analyses are based on data collected from 297 territories (128 in south-eastern Scotland, 169 in south-western Scotland) monitored during 1964–2015. Field workers attempted to visit every known Peregrine site (i.e. terrain feature or building that could hold one or more Peregrine nest locations) at least twice during the nesting season to determine occupancy and breeding output. They also checked new sites that, because of their distance from active sites and availability of nesting locations or based on word of mouth, might hold Peregrines. Generally, first eggs were laid in late March–early April so that first visits were made during March and April. At this time, it is often easy to determine whether a clutch has been started by the behaviour of the occupants, by climbing to the nest ledge or viewing it from a vantage point. At some sites, especially difficult ones, however, the results of this first visit were inconclusive, and further visits were required to determine breeding status.

If a site was occupied and eggs had been laid, an effort was made to determine final clutch size, providing this could be done without undue disturbance or revealing the site to unknown onlookers. In addition, some coastal nest locations were extremely difficult to access so clutch and brood sizes were often unknown. Nest-sites with eggs were revisited when it was judged they would have chicks old enough to ring (*c.* 2–4 weeks), mostly between 20 May and 20 June. The number of young present at this stage was taken as the number fledging. A territory was considered reproductively successful if it produced at least one chick.

The management of land for grouse at each site was determined by evidence in the field (e.g. burning of heather, existence of shooting butts) and local knowledge held by the field workers of estate activities and boundaries, and territories were categorized as being in areas 'actively managed for grouse' or 'not actively managed for grouse'.

Data in the eastern and western portions of the study area were collected by different observers. Given the differences between the east and west in landscapes, land use and weather (see above), we checked for differences in occupancy and reproductive success between the east and west. We also tested for the effect of region (east or west) on the probabilities of detection, occupancy and reproductive success (see below).

Occupancy modelling

We used a multi-season, multi-state occupancy modelling framework (MacKenzie *et al.* 2009, 2010) to estimate and model territory occupancy and reproductive success, and to test for the effects of covariates on these parameters. This modelling framework accounts for imperfect detection and allows estimation of the probability that a territory is occupied, and when occupied, whether it experienced reproductive success (i.e. fledged at least one chick). We considered three true occupancy states (m): (1) unoccupied ($m = 0$) for territories that were empty or with only a single bird in a particular year but had been occupied at least once by a Peregrine pair in the past, (2) occupied without successful reproduction ($m = 1$) when a territory was occupied by a Peregrine pair but no fledglings were produced, and (3) occupied with successful reproduction ($m = 2$) when a territory was occupied by a Peregrine pair and at least one chick fledged. In addition to the initial occupancy probability (ψ_0; probability that a territory was occupied during the first year of the study) and initial probability of reproductive success (R_0; probability that occupied territories experienced reproductive success), the model consisted of the following parameters (hereafter, dynamic occupancy parameters): ψ_t^m, which was the (conditional) probability of a territory being occupied by a Peregrine breeding pair in year t given that it was in state m in year $t-1$ (with $m = 0$, 1 or 2); R_t^m, which was the (conditional) probability of successful reproduction at an occupied territory in year t given that it was in state m in year $t-1$; ψ_t^1 and ψ_t^2 were the probabilities of detecting the species in the year t given that the territory is truly in state 1 or 2, respectively; and δ_t is the probability of observing the evidence of successful reproduction given the species has been detected and reproduction has occurred (MacKenzie *et al.* 2009, Martin *et al.* 2009).

Even though many sites/territories were visited several times during a breeding season, observers did not always keep track of the multiple visits made, and our database generally included a single observation per territory per year (especially for unoccupied sites) and had many missing observations (especially of follow-up visits to sites where occupancy or nesting was not confirmed early in the field season). To cope with the missing data, we classified sites on the basis of the likelihood of missing occupancy for each territory as measured by the level of confidence of the observers that they could accurately determine occupancy, and on the remoteness of the territories: 0 – if a territory was thought to be occupied, it would have been nearly impossible to miss it (e.g. traditional sites, which were surveyed every year); 1 – if a territory was presumed occupied, it would have been highly unlikely that observers could have missed it (e.g. territories close to traditional sites); 2 – observers were likely to have missed the occupancy initially because the site was not close or *en route* to traditional sites; and 3 – observers could easily have missed occupancy because of the remoteness or difficulty of access (e.g. large coastal cliffs and some man-made structures). We coded missing data as unoccupied (0) for territories for which it was nearly impossible to miss occupancy (e.g. traditional sites that were monitored regularly; values 0 and 1 for likelihood of missing occupancy) or unvisited (–) for territories that were likely to have been missed even when occupied due to the remoteness of the territories and/or difficulty of access (values 2 and 3 for likelihood of missing occupancy). For dealing with imperfect detection, we followed the methodology recommended by Lele *et al.* (2012) and Sólymos *et al.* (2012). These authors suggest that territory occupancy (or abundance) and detection probability parameters can be estimated using a single observation per year if: (1) probabilities of occupancy and detection depend on covariates, and (2) the set of covariates that affect occupancy and the set of covariates that affect detection differ by at least one variable. Consequently, we modelled the probability of detection as a constant parameter, and as a function of additive and interactive effects of occupancy state (occupancy with or without successful reproduction), and region (eastern or western parts of the study area); data were insufficient to support more complicated model structures. We modelled occupancy and reproductive probabilities during the first year of study (ψ_0 and R_0, respectively) as constant parameters, but also allowed them to be affected by region. Finally, the state-specific conditional probabilities of occupancy (ψ_t^0, ψ_t^1 and ψ_t^2), and the probabilities of successful reproduction (R_t^0, R_t^1 and ψ_t^2), conditional on occupancy, were modelled as constant parameters, and as functions of state, region, linear and quadratic temporal trends and interactions among these covariates, and an additive effect of the mean annual nearest neighbour distance (NND, normalized to zero mean, used as an index of population density), and habitat management for Red Grouse (managed or unmanaged). We calculated mean NND for each year as the mean of distances from each occupied territory to all other occupied territories in that year.

We used an information theoretic approach, based on Akaike's information criterion (AIC), for model selection and statistical inference (Burnham & Anderson 2002). Dynamic occupancy models were implemented in the program PRESENCE 10.9 (Hines 2011).

RESULTS

The number of occupied territories varied widely over time, ranging from eight in 1964 to 155 in 2014, with a generally increasing temporal trend (Fig. 2a). The naïve estimates of territory occupancy (the proportion of known territories that were occupied; this approach assumes a detection probability of 1.0) ranged from 0.24 in 1964 to 0.81 in 1991. Likewise, naïve estimates of reproductive success (the proportion of occupied sites that fledged ≥ 1 chick) ranged from 0.23 in 1967 to 0.81 in 2010 (Fig. 2b). The naïve territory occupancy increased initially, peaking around the 1990s, whereas the proportion of occupied territories experiencing reproductive success varied widely throughout the study period (Fig. 2b).

The most parsimonious dynamic occupancy model included no covariate effect on initial occupancy (ψ_0) and initial probability of reproduction (R_0), but included an effect of region on the probability of detection (p), an interactive effect of state, region, linear, and linear and quadratic temporal trends on the conditional probability of occupancy (ψ^m) and the conditional probability of reproduction (R^m) (Table 1). Logistic regression coefficients and real parameter estimates based on this model (Table 2, Figs 3 & 4) revealed that probability of detection was substantially higher for territories in south-east (0.95 ± 0.08) than in south-west Scotland (0.88 ± 0.01). The initial occupancy probability was 0.40 ± 0.08, whereas the initial probability of reproductive success was 0.60 ± 0.18; these parameters did not differ between regions. Initial occupancy (ψ_0) was higher for territories in south-east than in south-west Scotland, and increased steadily in both regions until the 1990s. The probability of occupancy of territories that experienced reproductive success the previous year (ψ^2) was generally higher in south-western than in south-eastern territories and increased steadily over time in both regions. The

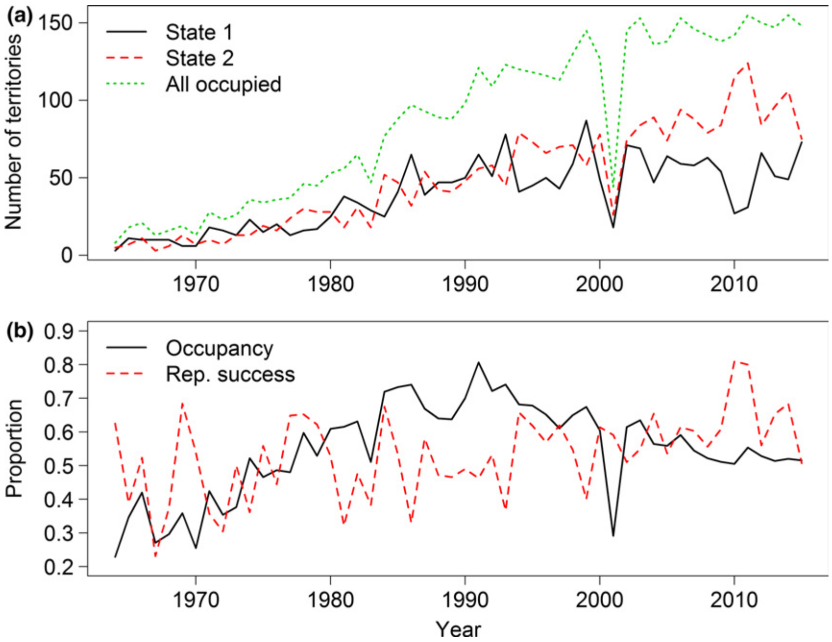

Figure 2. (a) The number of Peregrine territories that were occupied without successful reproduction (State 1) and with successful reproduction (State 2), and the total number of occupied sites (All occupied), and (b) naïve estimates of Peregrine occupancy (Occupancy) and reproductive success (Rep. success) in southern Scotland, 1964–2015). We had limited access to the breeding sites in 2001 due to the outbreak of foot and mouth disease. [Colour figure can be viewed at http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X]

Table 1. Model comparison statistics for multistate dynamic occupancy models for Peregrine Falcons in southern Scotland.

No.	Model	*K*	AIC	ΔAIC	AIC weight
1	ψ_0(.) R_0(.) ψ(state*region*T^2) R(state*region*T^2) p(region)	40	13 506.67	0.00	0.61
2	ψ_0(region) R_0(region) ψ(state*region*T^2) R(state*region*T^2) p(state*region)	44	13 509.80	3.13	0.13
3	ψ_0(.) R_0(.) ψ(state*region*T^2) R(state*region*T^2) p(state*region)	42	13 510.04	3.36	0.11
4	ψ_0(region) R_0(region) ψ(state*T^2) R(state*region*T) p(region)	27	13 511.57	4.89	0.05
5	ψ_0(.) R_0(.) ψ(state*T^2) R(state*region*T) p(state*region)	27	13 511.74	5.06	0.05
6	ψ_0(.) R_0(.) ψ(state*T^2) R(state*region*T) p(region)	25	13 512.64	5.97	0.03
7	ψ_0(region) R_0(region) ψ(state*T^2) R(state*region*T^2) p(region)	33	13 515.28	8.61	0.01
8	ψ_0(.) R_0(.) ψ(state*T^2) R(state*region*T^2) p(region)	31	13 517.94	11.27	< 0.01

Model parameters are: ψ_0, R_0 = initial occupancy and reproductive success probabilities, respectively; ψ = occupancy probability; R = probability of successful reproduction, conditional on occupancy, and p = detection probability. Covariates were: state = occupancy state (0 = unoccupied, 1 = occupied without successful reproduction, 2 = occupied with successful reproduction); region = location of a territory (south-eastern or south-western Scotland); T, T^2 = linear and quadratic trends, respectively. A full stop (.) indicates a constant parameter, and an asterisk (*) indicates both additive and interactive effects. The number of parameters (K), Akaike's information criterion (AIC), difference in AIC (ΔAIC) between the focal and lowest-AIC models, and model weights (AIC weight, relative likelihood of models in the set) are also presented. For all models, the parameter $\delta_{t,j}$ (the probability of observing the evidence of successful reproduction given the species has been detected and reproduction has occurred) was set to 1.0. All models with AIC weight $\geq$ 0.001 are presented. A complete model list, with associated model comparison statistics, is presented in Table S1 (Supporting Information).

probability of occupancy of territories that experienced reproductive failure the previous year (ψ^1) declined over time until the 1990s; it continued to decline in south-western but increased slightly in south-eastern territories (Fig. 3). R_0 and R^1 were generally higher for territories in the south-west than in the south-east, whereas R^2 was substantially higher in territories located in south-east Scotland. The pattern of temporal variation in R_0 differed between west and east. The probability of successful reproduction at occupied territories (R^1 and R^2) generally increased over time regardless of

Table 2. Logistic regression coefficients ($\beta \pm 1$ se) for the most parsimonious multi-state dynamic occupancy model (Model 1, Table 1).

		Covariates				
Parameter	Intercept	Region	T	T^2	Region*T	Region*T^2
Initial occupancy Ψ_0	−0.41 ± 0.33					
Initial probability of reproduction R_0	0.42 ± 0.73					
Conditional occupancy (Ψ^m)						
Ψ_0	−2.82 ± 0.33	0.82 ± 0.78	2.53 ± 0.60	−0.98 ± 0.22	−0.12 ± 1.13	−0.13 ± 0.38
Ψ^1	2.47 ± 0.47	−0.19 ± 1.12	−0.07 ± 0.67	−0.164 ± 0.22	−1.03 ± 1.47	0.53 ± 0.46
Ψ^2	2.58 ± 1.10	−1.56 ± 2.43	0.21 ± 2.12	0.23 ± 0.82	1.46 ± 4.08	−0.64 ± 1.43
Conditional probability of reproduction (R^m)						
R_0	0.21 ± 0.62	0.23 ± 1.23	−0.15 ± 0.96	−0.01 ± 0.34	−4.10 ± 1.55	1.92 ± 0.54
R^1	−0.52 ± 0.28	−0.77 ± 0.79	0.29 ± 0.41	−0.08 ± 0.14	0.32 ± 1.02	−0.04 ± 0.32
R^2	0.01 ± 0.27	−1.89 ± 1.04	0.59 ± 0.38	−0.08 ± 0.13	1.67 ± 1.26	−0.26 ± 0.37
Probability of detection (p)	2.04 ± 0.08	0.89 ± 0.25				

Parameters are: Ψ_0, R_0 = initial occupancy and initial probability of reproduction, respectively; Ψ^m, R^m = conditional state-specific occupancy and probability of reproduction, respectively; and p = probability of detection. The superscript in conditional occupancy and probability of reproduction parameters indicate state-specificity, with 0, 1 and 2 representing unoccupied, occupied without successful reproduction, and occupied with successful reproduction during the previous breeding season, respectively. Covariates are defined in Table 1. For the region covariate, south-west Scotland is used as a reference.

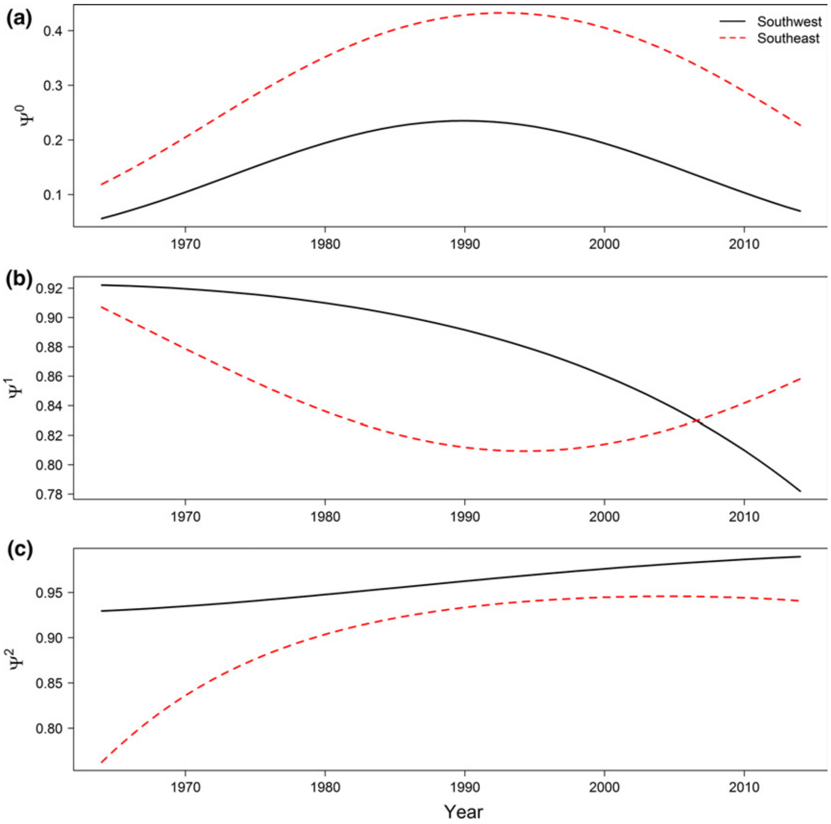

Figure 3. Temporal variation in state-specific conditional occupancy probabilities (Ψ^m) in southern Scotland, 1964–2015. The probability of occupancy of sites that were unoccupied (a), occupied without successful reproduction (b) and occupied with successful reproduction (c) in the previous year for each year of the study are presented. These relationships were estimated based on the most parsimonious dynamic occupancy model (Model 1, Table 1). [Colour figure can be viewed at http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X]

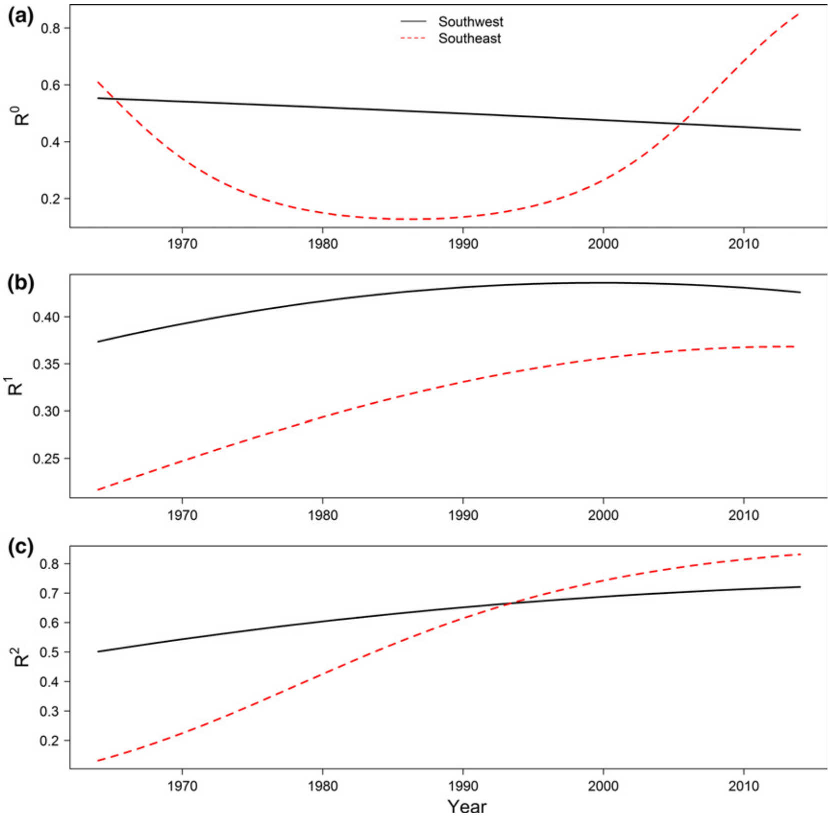

Figure 4. Temporal variation in state-specific conditional reproductive success probabilities (R^m) in southern Scotland, 1964–2015. The probability of reproductive success of occupied sites that were unoccupied (a), occupied without successful reproduction (b) and occupied with successful reproduction (c) in the previous year for each year of the study are presented. These relationships were estimated based on the most parsimonious dynamic occupancy model (Model 1, Table 1). [Colour figure can be viewed at http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X]

reproductive success the previous year; the increase in R^2 in eastern territories was particularly dramatic, ranging from 0.13 in 1964 to 0.83 in 2015 (Fig. 4). There was no evidence that dynamic occupancy and reproductive success differed between territories on land managed for grouse vs. those where the land was not managed for grouse, nor was there any evidence that these parameters were affected by NND. Habitat management and NND did not appear as covariates for ψ^i or R^i in well-supported models (Table 1).

DISCUSSION

We expected territory occupancy to increase as the population recovered from small numbers during the 1960s to 1970s when organochlorine pesticides were still in use, to recent years when the population is thought to have recovered fully from their effects (Crick & Ratcliffe 1995, Banks *et al.* 2010, Smith *et al.* 2015). Consistently, all well-supported models for ψ^m included an interactive effect of state, region and temporal trend, suggesting that the conditional occupancy probability varied over time and differed between the regions. However, the pattern of variation depended on whether the territory was occupied during the previous breeding season and, if occupied, whether young were produced (Tables 1 & 2, Fig. 3). Territories that were occupied and produced young the previous breeding season were substantially more likely to be occupied in the current year than were those that were unoccupied or occupied and had failed in the previous year. This pattern was as predicted because fidelity to territory is reduced in many raptorial birds following unsuccessful breeding attempts (Mearns & Newton 1984; Newton 1991, Sergio & Newton 2003, MacKenzie *et al.* 2010). Territories that were occupied and produced young the previous year increased steadily during the study period, although more rapidly in eastern (0.77 in 1964 to 0.94 in 2015) than in western areas (0.93 in 1964 to 0.99 in 2015) (Fig. 3). The probability of occupancy of territories that were unoccupied during the previous year also increased until the 1990s, as more potential territories were taken up. Peregrine densities were very low during the early years of our study as a result of the negative effects of organochlorine pesticides on survival and reproduction (Ratcliffe 1970, Peakall 1974, 1976, Newton 1979, Fry 1995) and persecution (Ratcliffe 2003). By 1963, the distribution of Peregrines had contracted and the population reached the lowest recorded levels (Ratcliffe 1993), so initially only a small number of territories were occupied in southern Scotland. Subsequently, progressive reduction in the use of organochlorines was followed by improved reproductive output and probably also by improved survival, contributing to a recovery of Peregrine numbers across Britain (Crick & Ratcliffe 1995, Banks *et al.* 2010, Smith *et al.* 2015); the increase in population size led to an increased probability of occupancy of previously unoccupied territories and those producing young during the previous breeding season. These results are consistent with findings from southern Scotland that Peregrines increasingly occupied new sites during 1975–82 and, once they were occupied, they generally remained occupied (Mearns & Newton 1988). The occupancy probability of territories that experienced reproductive failure during the previous breeding season generally declined over time (Fig. 3b). This pattern may be a consequence of increased competition for breeding sites as population density increased, and a general improvement in breeding success as the direct and residual effects of organochlorine pesticides disappeared from the population. Detection probability was higher in the east than in the west, perhaps because of the differences in ruggedness.

Many raptorial birds around the world experienced reproductive failure during the organochlorine era due to both fragility of eggs and deaths of embryos during incubation (e.g. Ratcliffe 1970, Cooke 1979, Newton 1979, Mearns & Newton 1988, Olsen *et al.* 1992). Eggshell thinning and consequent reproductive failure was widely documented prior to and during the Peregrine population decline and early stages of recovery in Scotland (Prestt & Ratcliffe 1967, Ratcliffe 1967, 1970, Newton 1979, Nisbet 1988), so we also expected reproductive success to increase as the direct and residual effects of organochlorine pesticides declined and ultimately disappeared from the population. Consistently, the probability of reproductive success (conditional on occupancy) of previously occupied territories (R^1 and R^2) increased steadily during the study period. This trend was particularly dramatic in south-eastern Scotland (R^1 increased from 0.22 in 1964 to 0.36 in 2015, and R^2 rose from 0.13 in 1964 to 0.83 in 2015), although it was non-trivial in south-western Scotland as well (R^1 increased from 0.37 in 1964 to 0.43 in 2015, and R^2 rose from 0.50 in 1964 to 0.72 in 2015). Our results support the view that reproductive failure attributable to organochlorine pesticides contributed to Peregrine population declines in southern Scotland. When our study started, the breeding range of Peregrines in Scotland was contracted, the population was at its lowest level and only 16% of the breeding pairs fledged young (Ratcliffe 1993); by the mid 1980s, reductions in organochlorine pesticide use resulted in a lessening of the effects on Peregrines (Newton *et al.* 1989). These observations are consistent with our findings that R^1 and R^2 were very low during the 1960s to 1970s, and increased steadily over time as the effects of organochlorines disappeared from the population.

Territories that were occupied by birds that produced young during the previous breeding season were substantially more likely to be occupied and be reproductively successful than those that were unoccupied or occupied without reproductive success in the previous year. In southern Scotland, where mark-recapture studies occurred during 1974–82 (Mearns & Newton 1988) and since 2002 (Smith *et al.* 2015), very few cases of successful breeders moving territories were recorded, and those that did move sometimes moved more than once. Some territories are almost always occupied, birds occupying such territories nearly always bred successfully, and when vacant, these territories are quickly re-colonized (Mearns & Newton 1988, Ratcliffe 1993). These findings suggest that Peregrines preferentially select territories where their chances of producing young are high – the territories with a history of good reproductive success. As the breeding population increased in southern Scotland, preferential occupancy of the best territories (with nest-sites difficult to access in areas with high food availability) progressively reduced the availability of such high-quality territories, causing a higher proportion of new colonizers to take suboptimal or non-traditional sites (e.g. more accessible cliffs and man-made structures; Mearns & Newton 1988, Banks *et al.* 2010). Typically, high-quality territories are occupied before low-quality ones, as the population increases (Newton 1998). The displacement of birds to poorer territories as abundance rises can cause a decline in the average breeding performance of the population, without a significant decline in breeding success in the better territories (Nilsson 1987, Ferrer 1993, Panek 1997, Newton 1998). As a result of this pattern of territory occupancy, the mean per-capita reproductive performance for the population can decline progressively in a density-dependent manner. Consequently, availability of territories could function in regulating the overall population level of Peregrines; availability of high-quality sites can be the limiting factor because it influences reproductive success (e.g. Rodenhouse *et al.* 1997, 2000, Gill *et al.* 2001).

The 1954 Protection of Birds Act gave most raptors full legal protection in the UK, and Peregrines and other raptors have been protected under the Council Directive 79/409/EEC on the Conservation of Wild Birds ('Birds Directive') since 1979 (UK Raptor Working Group 2000). Nevertheless, raptors in Scotland, including Peregrines, are still persecuted (RSPB 1995, 2015, North East Scotland Raptor Study Group 2015). The perception of Peregrines as a threat to game birds leads to an increased persecution by gamekeepers, so we expected a lower breeding success in territories in areas managed for grouse. Gamekeeping and hunting activities can disturb and potentially result in mortality of nesting birds (e.g. Hardey *et al.* 2003, Whitfield *et al.* 2003, Amar *et al.* 2012). However, the effect of managing areas for grouse on Peregrine reproductive success appears to have been less important in southern Scotland, at least during the early part of the study, compared with that of organochlorine pesticides. It should be noted, however, that persecution and intentional disturbance of falcons comes from a variety of sources, including individuals from the pigeon racing, game-hunting (including species other than grouse), falconry and egg-collecting communities (Dixon *et al.* 2003, Hardey *et al.* 2003, Ratcliffe 2003, Shawyer *et al.* 2003) and that the relative pressure and geographical pattern of effort by those individuals has changed across space and time. These characteristics of falcon persecution and disturbance, and the fact that the effects of persecution can mirror natural processes, make assessment of the impact of persecution over our study period difficult. Although the effects of organochlorine pesticides may have been more important in the past, this is certainly not the case now. Indeed, it may be that the importance of the effects of organochlorine pesticide contamination on Peregrine occupancy and reproduction during the early part of this study masks the effects of persecution, as reported by Hardey *et al.* (2003) and Amar *et al.* (2012); these studies overlapped less with the organochlorine era than did ours and occurred over different geographical areas. Currently, persecution may be impeding full recovery of the Peregrine populations in some areas, and the difficulties in quantifying it cloud our understanding of the natural factors limiting Peregrine numbers (Amar *et al.* 2012).

Models that included temporal trends were always preferred over those that included NND, suggesting that this index of abundance was insufficient to explain temporal variation in territory occupancy probabilities. Reproductive success is an important determinant of fitness as well as population growth rate (Clutton-Brock 1988, Newton 1989, Oli & Dobson 2003, Stahl & Oli 2006). For Peregrines, acquisition of a territory is a prerequisite for successful reproduction (Newton 1988, Ratcliffe 1993). Our results suggest that reproductive success was low during the pesticide era even in territories with a history of successful reproduction. Furthermore, the difference in the temporal pattern of state-specific reproductive success probabilities between south-east and south-west Scotland suggests that the effect of organochlorine pesticides on Peregrine reproductive success and/or the recovery from pesticide effects probably differed between these regions and possibly was affected by other factors, such as persecution. Although we have no quantitative data on the spatial or temporal pattern of organochlorine pesticide use in southern Scotland, south-eastern Scotland has more arable land, which is more evenly distributed than south-western Scotland. Newton *et al.* (1989) linked reduced brood sizes in Peregrines to levels of DDE, and showed that a north–south gradient in Peregrine decline matched the gradient in agricultural land. Taken together, these results are consistent with the idea that reproductive failure played an important role in Peregrine population declines and in limiting Peregrine population growth until the effects of organochlorine pesticides were sufficiently reduced. Peregrine Falcons are much more common now than they once were (Banks *et al.* 2010) and long-term studies such as ours permit retrospective assessments of how wildlife populations respond to anthropogenic perturbations to the natural environment.

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REFERENCES

Amar, A., Court, I.R., Davison, M., Downing, S., Grimshaw, T., Pickford, T. & Raw, D. 2012. Linking nest histories, remotely sensed land use data and wildlife crime records to explore the impact of grouse moor management on Peregrine Falcon populations. *Biol. Conserv.* **145**: 86–94.

Bailey, L.L., MacKenzie, D.I. & Nichols, J.D. 2014. Advances and applications of occupancy models. *Methods Ecol. Evol.* **5**: 1269–1279.

Banks, A.N., Crick, H.Q.P., Coombes, R., Benn, S., Ratcliffe, D.A. & Humphreys, E.M. 2010. The breeding status of Peregrine Falcons *Falco peregrinus* in the UK and Isle of Man in 2002. *Bird Study* **57**: 421–436.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. New York, NY: Springer.

Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. 1988. *Peregrine Falcon Populations: Their Management and Recovery*. Boise, ID: The Peregrine Fund.

Clutton-Brock, T.H. 1988. Reproductive success. In Clutton-Brock, T.H. (ed.) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*: 472–485. Chicago, IL: University of Chicago Press.

Cooke, A.S. 1979. Changes in egg shell characteristics of the Sparrowhawk (*Accipiter nisus*) and Peregrine (*Falco peregrinus*) associated with exposure to environmental pollutants during recent decades. *J. Zool.* **187**: 245–263.

Crick, H.Q.P. & Ratcliffe, D.A. 1995. The Peregrine *Falco peregrinus* breeding population of the United Kingdom in 1991. *Bird Study* **42**: 1–19.

Dixon, A., Richards, C., Lawrence, A. & Thomas, M. 2003. Peregrine (*Falco peregrinus*) predation on racing Pigeons (*Columba livia*) in Wales. In Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (eds) *Birds of Prey in a Changing Environment*: 255–262. Edinburgh: Scottish Natural Heritage.

Enderson, J. & Berger, D. 1970. Pesticides: eggshell thinning and lowered production of young in Prairie Falcons. *Bioscience* **20**: 355–356.

Ferrer, M. 1993. *El Águila Imperial*. Madrid: Quercus.

Fry, D.M. 1995. Reproductive effects in birds exposed to pesticides and industrial chemicals. *Environ. Health Perspect.* **103**: 165–171.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. 2001. The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**: 436–438.

Hardey, J., Rollie, C.J. & Stirling-Aird, P.K. 2003. Variation in breeding of inland Peregrine Falcon (*Falco peregrinus*) in three regions of Scotland 1991–2000. In Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (eds) *Birds of Prey in a Changing Environment*: 99–110. Edinburgh: Scottish Natural Heritage.

Heath, R.G., Spann, J.W. & Kreitzer, J.F. 1969. Marked DDE impairment of Mallard reproduction in controlled studies. *Nature* **224**: 47–48.

Hines, J.E. 2011. *PRESENCE 10.9 – Software to Estimate Patch Occupancy and Related Parameters*. Available at: http://www.mbr-pwrc.usgs.gov/software/presence.html (accessed 10 June 2016).

Lele, S.R., Moreno, M. & Bayne, E. 2012. Dealing with detection error in site occupancy surveys: what can we do with a single survey? *J. Plant Ecol.* **5**: 22–31.

MacKenzie, D.I., Nichols, J.D., Seamans, M.E. & Gutiérrez, R.J. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* **90**: 823–835.

MacKenzie, D.I., Seamans, M.E., Gutiérrez, R.J. & Nichols, J.D. 2010. Investigating the population dynamics of California Spotted Owls without marked individuals. *J. Ornithol.* **152**: 597–604.

Martin, J., McIntyre, C.L., Hines, J.E., Nichols, J.D., Schmutz, J.A. & MacCluskie, M.C. 2009. Dynamic multistate site occupancy models to evaluate hypotheses relevant to conservation of Golden Eagles in Denali National Park, Alaska. *Biol. Conserv.* **142**: 2726–2731.

Mearns, R. & Newton, I. 1988. Factors affecting breeding success of Peregrines in south Scotland. *J. Anim. Ecol.* **57**: 903–916.

Newton, I. 1974. Changes attributed to pesticides in the nesting success of the Sparrowhawk in Britain. *J. Appl. Ecol.* **11**: 95–101.

Newton, I. 1979. *Population Ecology of Raptors*. Berkhamsted: T. and A.D. Poyser.

Newton, I. 1988. Population regulation in peregrines: an overview. In Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (eds) *Peregrine Falcon Populations: Their Management and Recovery*: 761–770. Boise, ID: The Peregrine Fund.

Newton, I. 1989. *Lifetime Reproduction in Birds* (Newton, I., ed.). London: Academic Press.

Newton, I. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis* **133**(S1): 76–88.

Newton, I. 1998. *Population Limitation in Birds*. London: Academic Press.

Newton, I. & Mearns, R. 1988. Population ecology of Peregrines in south Scotland. In Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (eds) *Peregrine Falcon Populations: Their Management and Recovery*: 651–665. Boise, ID: The Peregrine Fund.

Newton, I., Bogan, J.A. & Haas, M.B. 1989. Organochlorines and mercury in the eggs of British Peregrines *Falco peregrinus*. *Ibis* **131**: 355–376.

Nilsson, S. 1987. Limitation and regulation of population density in the Nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *J. Anim. Ecol.* **56**: 921–937.

Nisbet, I.C.T. 1988. The relative importance of DDE and dieldrin in the decline of Peregrine Falcon populations. In Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (eds) *Peregrine Falcon Populations: Their Management and Recovery*: 351–375. Boise, ID: The Peregrine Fund.

North East Scotland Raptor Study Group 2015. Peregrines in north-east Scotland in 2014 – further decline in the uplands. *Scott. Birds* **35**: 202–206.

Oli, M.K. & Dobson, F.S. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *Am. Nat.* **161**: 422–440.

Olsen, P., Emison, B., Mooney, N. & Brothers, N. 1992. DDT and dieldrin: effects on resident Peregrine Falcon populations in south-eastern Australia. *Ecotoxicology* **100**: 89–100.

Panek, M. 1997. Density-dependent brood production in the Grey Partridge *Perdix perdix* in relation to habitat quality. *Bird Study* **44**: 235–238.

Peakall, D. 1970. Pesticides and the reproduction of birds. *Sci. Am.* **222**: 72–78.

Peakall, D.B. 1974. DDE: its presence in Peregrine eggs in 1948. *Science* **183**: 673–674.

Peakall, D.B. 1976. The Peregrine Falcon (*Falco peregrinus*) and pesticides. *Can. Field Nat.* **90**: 301–307.

Peakall, D.B., Reynolds, L.M. & French, M.C. 1976. DDE in eggs of Peregrine Falcon. *Bird Study* **23**: 183–186.

Porter, R.D. & Wiemeyer, S.N. 1969. Dieldrin and DDT: effects on Sparrowhawk eggshells and reproduction. *Science* **165**: 199–200.

Prestt, I. & Ratcliffe, D.A. 1967. Effects of organochlorine insecticides on European birdlife. *Proc. Int. Ornithol. Congr.* **15**: 486–513.

Ratcliffe, D.A. 1967. Decrease in eggshell weight in certain birds of prey. *Nature* **215**: 208–210.

Ratcliffe, D.A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. *J. Appl. Ecol.* **7**: 67–115.

Ratcliffe, D. 1993. *The Peregrine Falcon*. Berkhamsted: T. and A. D. Poyser.

Ratcliffe, D.A. 2003. The Peregrine saga. In Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (eds) *Birds of Prey in a Changing Environment*: 91–98. Edinburgh: Scottish Natural Heritage.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* **78**: 2025–2042.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. 2000. Site-dependent regulation of population size: reply. *Ecology* **81**: 1168–1171.

RSPB 1995. *Bird of Prey Persecution in Scotland in 1994*. Edinburgh: RSPB Scotland.

RSPB 2015. *The Illegal Killing of Birds of Prey in Scotland 1994–2014: A Review*. Edinburgh: RSPB Scotland.

Sergio, F. & Newton, I. 2003. Occupancy as a measure of territory quality. *J. Anim. Ecol.* **72**: 857–865.

Shawyer, C.R., Clarke, R. & Dixon, N. 2003. Causes of racing Pigeon (*Columba livia*) losses, including predation by raptors in the United Kingdom. In Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (eds) *Birds of Prey in a Changing Environment*: 263–268. Edinburgh: Scottish Natural Heritage.

Smith, G.D., Murillo-Garcia, O.E., Hostetler, J.A., Mearns, R., Rollie, C., Newton, I., McGrady, M.J. & Oli, M.K. 2015. Demography of population recovery: survival and fidelity of Peregrine Falcons at various stages of population recovery. *Oecologia* **178**: 391–401.

Sólymos, P., Lele, S.R. & Bayne, E. 2012. Conditional likelihood approach for analyzing single visit abundance survey data in the presence of zero inflation and detection error. *Environmetrics* **23**: 197–205.

Stahl, J.T. & Oli, M.K. 2006. Relative importance of avian life-history variables to population growth rate. *Ecol. Model.* **198**: 22–39.

UK Raptor Working Group 2000. *Report of the UK Raptor Working Group*. UK Department of the Environment, Transport and the Regions and the Joint Nature Conservation Committee. Peterborough, UK: Joint Nature Conservation Committee.

Whitfield, D.P., McLeod, D.R.A., Watson, J., Fielding, A.H. & Haworth, P.F. 2003. The association of grouse moor in Scotland with the illegal use of poisons to control predators. *Biol. Conserv.* **114**: 157–163.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Model comparison statistics for multi-state dynamic occupancy models for Peregrine Falcons in southern Scotland.