

# Spatio-temporal variation in post-recovery dynamics in a large Peregrine Falcon *Falco peregrinus* population in the Jura mountains 2000–2020

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\* This article is dedicated to the dean of Swiss peregrinology, Gabriel ("Gaby") Banderet, who passed away on 23 August 2020.

After spectacular population crashes in the 1960-70s, Peregrine Falcons *Falco peregrinus* recovered worldwide, and in the 2000s many study populations were back to normal. However, post-recovery trends have been documented less well. We combined three long-term population studies covering the entire Jura mountains (16,304 km<sup>2</sup>) to examine spatio-temporal variation in population dynamics during 2000–2020 in 420 known nesting sites in five regions: Ain, Jura and Doubs in France, and Jura Sud and Jura Nord in Switzerland. Every year about 60% of all sites were surveyed at least once, and this proportion increased over time. We used Bayesian occupancy modeling to investigate site persistence and colonization probabilities and correct status and trend estimates for bias due to nonrandom site coverage. Based on the average of two models correcting or preferential sampling, we estimated that population size peaked in 2002 (Jura), 2005 (Doubs), 2007 (Ain, Jura Nord) and in 2007 for the Jura as a whole. Thereafter, the population declined significantly in four regions and in the Jura as a whole, with the strongest decline found in the Jura Nord (–38%, CRI –34%/–41%) during 2007–2020. Thus, we found considerable spatial heterogeneity in post-recovery trends and widespread post-recovery declines. Reasons for the latter may include eagle owl predation, illegal persecution, and human disturbance. Our results illustrate how quickly positive population trends may be reversed, such that continuous long-term monitoring even for species seemingly "out of danger" remains invaluable. Our study also emphasizes the importance of correcting for both coverage bias in general and for preferential sampling in particular when assessing population trends in studies where not every territory can be surveyed in all years.

**Keywords:** colonization rate, extinction rate, JAGS, occupancy model, persistence rate, pesticide victim; preferential sampling, population trend

Pesticide-induced population crashes of fish- and bird-feeding raptors in the second half of the last century provide some of the most well-known and -publicized examples of population declines in avian ecology and conservation, and perhaps in all of biodiversity conservation (Newton & Haas 1984, Ratcliffe 1993, Newton 1979, 1998, Bretagnolle *et al.* 2008). However, and contrary to so many other examples of large-scale population declines, they were later followed by almost equally remarkable recoveries in most species concerned once the main cause of the problem (pesticides) was recognized and removed (Sielicki & Mizera 2009, Balmer *et al.* 2013, Rau *et al.* 2015).

Arguably, the most renowned example of such a species is the worldwide-distributed Peregrine Falcon *Falco peregrinus*. Between the 1950s and the 1970s, its populations crashed, sometimes to regional extinction, in virtually every place from where adequate data exist (Hickey 1969, Fyfe *et al.* 1976, Cade *et al.* 1988, Ratcliffe 1993). However, around the turn of the century levels of many populations were back to normal (Cade *et al.* 1988, Cade & Burnham 2003, Sielicki & Mizera 2009, Ambrose *et al.* 2016, Bruggemann *et al.* 2015, 2016, Zuberogoitia *et al.* (2018), Kéry & Zuberogoitia 2020) and sometimes became even greater than recorded at any time before the pesticide crash (Horne & Fielding 2002, White *et al.* 2013, McGrady *et al.* 2017, Beran *et al.* (2018), Prommer & Bagyura (2018), Swem & Matz 2018; Wilson *et al.* 2018, Newton 2021). As a result, the threat category of the Peregrine in many national Red Lists was repeatedly changed to reflect reduced or even eliminated threat for extinction (Mesta 1999).

However, fewer published studies have examined the post-recovery population dynamics of former "pesticide victims" such as the Peregrine (but see the collection of papers from the 2017 Peregrine World Conference in Budapest, published 2018 in *Ornis Hungarica* ([sciendo.com/issue/ORHU/26/2](https://doi.org/10.23822/ornis.hungarica.2017.001)), an Swem & Matz (2018) and Franke *et al.* (2019)). This is regretful because on the one hand, the decades since the early 2000s may provide the first opportunity to study Peregrine population dynamics under somewhat undisturbed, "natural" conditions. On the other hand, new threats may arise; therefore continued demographic study of the former pesticide victims may be valuable as a sort of horizon-scanning for the species involved, but also for general biodiversity surveillance, since newly developed pesticides of other threats may affect them along with other species at the same time. In addition, populations of some rare meso and top predators may be more easy to survey than those of species lower down in the food-chain.

Here, we study the post-recovery dynamics in a large Peregrine population in Western Europe in the Jura mountains shared between France and Switzerland. We combine data from

three ongoing, large-scale population surveys that between them cover the entire Jura mountains of about 16,000 km<sup>2</sup>. The Peregrine reaches high densities in this mountain range, and its population has previously been shown to have fully recovered by the early 2000s (Monneret 2017, Kéry *et al.* 2018, Monneret *et al.* 2018). Our data comprise a total of 420 known nesting territories, or breeding sites, during the 21 years of 2000–2020. To assess spatial variation in population dynamics, we distinguished five geographical strata (or regions), which are defined by the intersection of the three surveys and political boundaries in France: the French Départements Ain, Jura and Doubs and the Swiss "Jura Sud" and "Jura Nord" study areas. To better understand the site-level demographic processes underlying population change, we use dynamic occupancy models (MacKenzie *et al.* 2003, Royle & Kéry 2007) to estimate probabilities of site persistence and site colonization, and their dependence on spatial and temporal covariates. To correct population size assessments for coverage or non-visitation bias (many sites were not visited in every year), we use Bayesian model-based imputation to estimate the most likely status (occupied or not) of a site for each year when data are lacking (Monneret *et al.* 2018; Kéry & Royle 2016, 2021).

An additional focus of this paper is preferential sampling (PS), which denotes a situation where the probability that a site is surveyed in some way depends on its "quality" (Diggle *et al.* 2010, Pacifici *et al.* 2012, 2016, Conn *et al.* 2017; Fandos *et al.* 2021). Most commonly it is the better sites, which are more likely to hold a pair or to produce young, that will be surveyed in preference to inferior sites that are known or believed to be less likely to be occupied or to have successful reproduction. When not all sites in a population can be surveyed every year, then this (possibly unconscious) sample selection process leads to a coverage bias that is non-random with respect to key site characteristics of interest, such as the presence or absence of a pair. Simple, random imputation of the status of sites with missing data will then fail (Monneret *et al.* 2018), and the non-random nature of site visitation must then be modelled jointly with the observed presence/absence patterns at the visited sites to properly impute the missing survey data. When PS is not accounted for in a model that estimates population size by extrapolating results from the surveyed to the unsurveyed sites, population size estimates will become too high (Conn *et al.* 2017; Monneret *et al.* 2018; Fandos *et al.* 2021; Kéry & Royle 2021, p. 272–284 & 385–397) and trend estimates may be biased. This is a widespread challenge for population studies such as ours. In this study we compare population size assessments that are based on the raw, observed data with those that use random imputation of missing data, i.e., that ignore potential PS, and those that achieve non-random imputation by using a model-based correction for PS.

In summary, in a large Western European Peregrine population we aim to identify the years when the post-pesticide peak population sizes were reached and to assess the post-peak population trajectories along with the demographic rates that govern population change at the level of an occupied site: site persistence and site colonization. We also study spatial variation by defining five strata or regions within the whole Jura mountains. In addition, we test and correct for the effects of a type of nonrandom coverage bias caused by PS.

## **METHODS**

### ***Study area***

Our study comprised the entire Jura mountains, a middle-elevation limestone mountain range on the border between France and Switzerland, which extends over more than 300 km and is about 100 km wide in East-West direction. Elevation ranges from about 200 m to 1718 m in a temperate region exposed to oceanic weather conditions. The Jura mountains are fairly sparsely populated by humans and almost 50% covered by forest. The remainder are mostly pastures, while arable land is rare, except along the low-lying fringes. Limestone cliffs suitable for nesting Peregrines are common throughout most of the mountain range. The French side of the Jura is shared by the three Départements Ain, Jura and Doubs, while on the Swiss side we distinguish the Southern and the Northern parts based on the two monitoring schemes there; see below. We applied a variant of the method of Ratcliffe (1962) to delimit the area inhabited by a Peregrine population by adding a buffer strip of half the mean nearest-neighbor distance to a hull defined by the locations of all pairs. This yielded areas of 2965, 3937 and 4558 km<sup>2</sup>, respectively, for Dép Ain, Dép Jura and Dép Doubs, for a total area of 11,460 km<sup>2</sup> on the French side of the Jura mountains, and of 1926 and 2919 km<sup>2</sup> for the Jura Sud and the Jura Nord, for a total of 4845 km<sup>2</sup> on the Swiss side of the Jura mountains. The entire study area thus covered 16,304 km<sup>2</sup>; see Fig. 1 and Table 1 for the definition of the study area and its regional strata.

We combined data collected in three separate, ongoing Peregrine population surveys which between them cover the entire Jura mountains and permit a long-term, range-wide population assessment of the Peregrine (Fig. 1). The first population study ("French Jura") comprises the entire French part of the Jura mountains and was initiated by René-Jean Monneret, René Ruffinoni and their colleagues in 1965 (Monneret 2006, 2017, Monneret *et al.* 2018). The second population study ("Jura Sud") is located in the Swiss Jura mountains and in adjacent regions of the Swiss plateau and along the northern edge of the Swiss Alps. It was launched by

Gaby Banderet and his colleagues in 1960. Here, and unlike in Kéry *et al.* (2018), we only use data from the Jura part of the Jura Sud. The third population study ("Jura Nord") is located in the central, northern and eastern parts of the Swiss side of the Jura mountains and was launched in 2005 by the first author. See Fig. 1 and Monneret *et al.* (2018) for a map of the French Jura study and Kéry *et al.* (2018) for maps of the areas of the full Banderet study and the Jura Nord. Here, we used data from 2000–2020 from the French Jura and the Jura Sud and from 2005–2020 from the Jura Nord. In total, we surveyed 420 nest sites or territories.

### **Field methods**

We use Peregrine "site" to define a cliff, building, or group of cliffs/buildings that has held at most one pair in any one year; inter-site spacing was usually more than 1 and more typically at least 2-3 km. Nesters on buildings were included, but with about 10 sites are currently very rare in our study area. The field protocol was essentially identical in all three studies, though survey intensity may have differed. During each breeding season (February–June) as many Peregrine sites as possible were surveyed by highly experienced volunteers in the three study groups to assess site occupancy and reproductive success. Surveys in February/March aimed to assess site occupancy, those in March/April checked for incubating birds at sites with viewable eyries, and those in April/May/June assessed productivity by counting large young in the nest or that were recently fledged. Sites were surveyed with 8–12x binoculars and 20–60x telescopes from distances between about 100 m and 4.8 km.

Most sites that were surveyed in a given year were surveyed multiple times. Thus, in the Jura Sud during 2000–2020, the number of surveys per site and year ranged from 0–31, with an average of 4.2. We don't know these statistics for the other two studies but think they may be slightly inferior. Unfortunately, the results of each survey are not available in computerized format; only the aggregate results of all surveys to a site within a breeding season. Hence, formal methods to account for false-negative survey errors using occupancy models with imperfect detection cannot be adopted (MacKenzie *et al.* 2002). Rather, we had to make the usual "index assumptions" in our analyses (Johnson 2008, Chapters 1 in Kéry & Royle 2016, 2021): that detection probability was either perfect or at least that its variation was uncorrelated with the spatiotemporal patterns that we are interested in, and hence, that our failure to formally account for detection probability did not materially affect our conclusions.

We took an occupied site to be one where a Peregrine pair was observed at least once during a breeding season. The basic data used here is a 420 x 21 binary matrix  $\mathbf{Y}_{i,t}$  of dimension site x year. It contains a 1 when site  $i$  was visited at least once and a pair was found during breeding season  $t$ , a 0 when no pair was found at a site visited at least once, and a missing value (NA) when site  $i$  had no recorded visit during year  $t$ .

In the Swiss Jura Sud, there was an interruption with virtually no field work at the habitual 29 sites in 2017/2018. The survey was relaunched in 2019 and 2020 and extended to 40 sites, of which 39 were surveyed in 2019 and all were in 2020. Thus, even with our model-based correction for coverage bias (see below) the results for the Jura Sud may not be entirely comparable before and after the 2017/2018 hiatus.

***Occupancy modeling to assess site-level population dynamics and to correct population size estimates for random or non-random coverage bias***

We used occupancy modeling for inferences about abundance changes and the underlying demographic mechanisms in Jura Peregrines (MacKenzie *et al.* 2017; Chapter 4 in Kéry & Royle 2021). To investigate population dynamics mechanisms we first fit a dynamic occupancy model (MacKenzie *et al.* 2003, 2017) to the site-by-year detection/nondetection data  $\mathbf{Y}_{i,t}$ . Dynamic occupancy models are hidden Markov models that explain the observed inter-annual transitions between the presence and absence of a Peregrine pair at a site as a function of persistence and colonization events, which are treated as random processes governed by probabilities of persistence and colonization (MacClintock *et al.* 2020). Combined with a simple model for the initial state of a binary system described in terms of occupancy probability, a tremendously flexible and powerful framework arises for the study of distribution or territory occupancy dynamics; see Chapter 4 in Kéry and Royle (2021) for a recent synthesis.

Specifically, for the first year in our study we assumed that whether site  $i$  was occupied ( $z_{i,2000} = 1$ ) or not ( $z_{i,2000} = 0$ ) is a Bernoulli random variable governed by the initial occupancy probability  $\psi_i$ :

$$z_{i,2000} \sim \text{Bernoulli}(\psi_i)$$

For later years, the presence or absence of a pair in year  $t = 2001 \dots 2020$  is described as a function of presence/absence of a pair in year  $t - 1$  and two random processes as follows: an

occupied site will remain occupied with a probability that we call persistence, and an unoccupied site will become occupied with a probability that we call colonization. We can describe both processes in a single algebraic expression with a logical "switch":

$$z_{i,t+1} | z_{i,t} \sim \text{Bernoulli}(z_{i,t}\phi_{i,t} + (1 - z_{i,t})\gamma_{i,t}).$$

Hence, if a site was occupied in the previous year, it will remain occupied this year with persistence probability  $\phi_{i,t}$ , while if it was not occupied, it will become occupied with colonization probability  $\gamma_{i,t}$ . These three random processes together comprise what we call the state process of the model.

Typical dynamic occupancy models also have an observation model that links the true state  $z$  with the observed state  $y$  in a probabilistic manner and can account for false-negative and/or false-positive errors (MacKenzie *et al.* 2003, Royle & Link 2006, Miller *et al.* 2011, Chambert *et al.* 2015). However, extra information is required to separately estimate the parameters in the state and the observation process, typically in the form of replicated surveys within a short interval where "closure" (i.e., no state change) is assumed or time-to-detection information (Kéry & Royle 2016, p. 617–621). As we did not have the replicate data required to estimate detection probability of an occupied site, we had to assume that detection probability was close to 1 and in particular, did not change systematically between our main dimensions of comparison: regions and years (see Chapter 1 in Kéry & Royle 2021). Detection probability of Peregrine pairs during the breeding season can be fairly high (Kéry & Royle 2016, p. 617–621) and will get higher still combined over multiple visits. Hence, we would expect the combined detection probability per site and year to be greater than 90% in our study for most sites that were visited at least once in a year. Thus, we will ignore any slight bias induced by our inability to estimate detection probability from the aggregated results in our surveys.

Above, initial occupancy probability is indexed by site  $i$  and persistence and colonization probability by both site  $i$  and yearly interval  $t$ . Hence, all three parameters can be modelled in GLM-manner by covariates that vary along these dimensions. We were interested in exploring spatiotemporal patterns in persistence and colonization. Hence, we fit a model where we allowed initial occupancy probability to differ by region. For persistence and colonization we allowed for categorical effects of region (fixed) and site (random) and with a random-walk smoother of year (see Chapter 13 in Link & Barker 2010, and Section 4.11. in Kéry & Royle 2021). In the latter, we treat first-order differences in a time-series of a parameter as a Gaussian random variable, as this can greatly enhance our ability to detect temporal patterns.

Not all 420 known Peregrine sites in the Jura were visited in each year and hence, to obtain unbiased estimates of population size, we needed to estimate the status of a site in every year it was not surveyed. In principle, such imputation of a missing value to correct for random non-visitation or *coverage bias* is really easy in Bayesian model-fitting by MCMC (see below; Monneret *et al.* 2018). However, to correct population size estimates for potentially *non-random coverage bias*, i.e., for preferential sampling (Diggle *et al.* 2010, Pacifici *et al.* 2012, 2016, Conn *et al.* 2017, Monneret *et al.* 2018; Fandos *et al.* 2021), we must model site occupancy jointly with site visitation. Otherwise, if the likelihood with which a site is surveyed depends in some way on whether it is occupied by a pair or not, then an occupancy model that does not take into account this non-ignorable missing-value generating process (Rubin 1976, Gelman *et al.* 2003) will suffer from bias in the estimates of population size and trends.

The solution to correct for non-random coverage bias is to model the detection/nondetection data  $\mathbf{Y}_{i,t}$  jointly with the corresponding indicators of site visitation,  $\mathbf{R}_{i,t}$ , and to link the two submodels for site occupancy by the falcons and site visitation by the human observers. This is done in a regression manner such that some measure of latent site quality is treated as a covariate, with coefficient  $\kappa$  (kappa), for the probability of site visitation (Conn *et al.* 2017). As in Monneret *et al.* (2018), we corrected for PS not in a dynamic occupancy model, but in a multi-year, "static" model, i.e., where annual changes are described by parameters that are stratified by year, without explicit description of the dynamics. We explored two occupancy models that accounted for PS: one which assumed a long-term quality assessment for a site and the other which assumed an "immediate behavioural response" of the observer to recent, perceived site quality. In the former (which we call PS model variant 1), we fit a Gaussian random site effect on the logit transform of annual occupancy probability. Here, we assume there is some average site quality that affects the likelihood with which a site is visited. In PS model variant 2, we used the presence/absence of a pair during the previous year as a predictor for visitation probability. As a benchmark for comparison, we also fit a variant of the static, multi-year occupancy models without a PS component to gauge the likely errors when erroneously assuming that coverage bias was random.

Thus, in total we fit four occupancy models to Peregrine detection/nondetection data  $\mathbf{Y}_{i,t}$  and their visit-indicator "data variant"  $\mathbf{R}_{i,t}$  :

- **Model 1** is the dynamic model fit only to  $\mathbf{Y}_{i,t}$ , and with which we gained insights into the spatiotemporal patterns of persistence and colonization probability.

- **Model 2** is the basic multi-year, static model assuming random site visitation which was also fit only to  $Y_{i,t}$ . We used it for a first set of population size estimates that corrected for coverage bias in a random manner.
- **Models 3 and 4** are the extensions of model 2 that jointly model site occupancy and site-visitation as just described; i.e., these models utilized both  $Y_{i,t}$  and  $R_{i,t}$ . Model 3 considers a persistent and time-constant effect of site quality on visitation probability, while model 4 assumes an immediate, short-term effect of the previous year's occupancy status only.

We used JAGS (Plummer 2003) to fit all models by running it from R using package jagsUI (Kellner 2016). Except for the PS coefficient  $\kappa$  in models 3 and 4, we specified vague priors for all parameters and ran the Markov chains for sufficiently long that convergence was reached based on the Brooks-Gelman-Rubin statistic (Gelman *et al.* 2003). We present posterior means for point estimates and 2.5 and 97.5 percentiles for 95% credible intervals (CRIs).

We have found that in some occupancy models with PS, the likelihood appears to be multimodal (see Chapter 6 in Kéry & Royle 2021) and a sign constraint may be necessary on the PS coefficient to resolve this special case of unidentifiability. Thus, we specified non-negative priors for the PS coefficients  $\kappa$ , since *if* there is non-random visitation, then we are virtually bound to find positive PS. We provide the specifications in the BUGS language (Lunn *et al.* 2013) of all our models in the Appendix.

To test for significant trends in population size, we fit linear regression models to all posterior samples of the  $N$  parameters and thus obtained a posterior distribution of slope estimates. A trend was considered significant if its central 95% percentiles did not include zero (Weir *et al.* 2009; van Strien *et al.* 2010, 2011, 2013).

## RESULTS

Over 61 years (1960–2020) a total of 420 Peregrine sites were recorded in the Jura mountains: 92, 94 and 100 in the French Dép of Ain, Jura and Doubs, for a total of 286 in the French Jura, and 41 and 93 in the Jura Sud and Jura Nord, respectively, for a total of 134 in the Swiss Jura (Fig. 1). Almost all sites were in cliffs (407), 10 on buildings, and three sites over the years had nests on both cliffs and buildings. Based on average site coordinates, the nearest-neighbour distance ranged from 0.7 to 14.4 km, with a median of 2.7 and a mean of 3.1 km. During 2000–2020, between 40 and 90 sites were surveyed annually in each of the three départements in the French Jura, with a slow increase over the years, which was however steeper in the Dép Doubs (Fig. 2). In

the Swiss Jura Sud, a stable number of 27–29 sites were surveyed annually through 2016, then only a single site in 2017 and 2018, but 39 sites in 2019 and 40 in 2020. In the Jura Nord, the number of surveyed sites increased from 60 in 2005 to around 80 in 2008 and all later years.

Observed population sizes (Fig. 2) in all five regions mirrored the trajectories of the number of surveyed sites, but at a lower level. The observed ("raw") population sizes were broadly in the range of 40–70 pairs in the Dép Ain Jura and Doubs, 20 – 30 in the Swiss Jura Sud, , while in the Swiss Jura Nord, 63 pairs were counted in 2007, but only around 40 pairs during 2013–2020. Altogether in the Jura mountains, the observed (= raw) number of Peregrine pairs (i.e., without imputation) increased from about 190 in 2000/2001 to a maximum count of 278 in 2008, then declined to 211 counted pairs in 2016, and increased again to 266 in 2020.

Dynamic occupancy modeling revealed high and stable values of persistence probability (Fig. 3, top) around 0.9 in all five regions until about 2005, followed by a very slight decline in the French Jura. This contrasted strongly with the Swiss Jura, where, in the Jura Sud, persistence dropped to about 0.75 within 10 years, while in the Jura Nord it was reduced from 0.94 to 0.71, albeit with signs of a weak recovery later. Colonization probability (Fig. 3, bottom) was more variable with stable fluctuations broadly between 0.20 and 0.50 in Dép Ain, Dép Jura, Dép Doubs, and Jura Sud. The Jura Nord was again an exception, where colonization dropped from 0.30 in 2006 to 0.15 during 2011–2019.

Fitting occupancy models with PS revealed strong evidence for a positive, but geographically varying strength of a "behavioural response" of the observers to either the long- or the short-term perceived quality of a site (Tab. 2). Under model 3 (which specified an effect of long-term site quality), estimates of the PS coefficient  $\kappa$  ranged from 1.41 in the Dép Ain to 0.23 in the Jura Nord, while under model 4 (with an immediate, or short-term effect of site-quality), estimates ranged from 3.28 in Jura Sud to 0.95 in the Jura Nord. Owing to the overwhelming evidence for PS and our indecision as to which PS model was preferable, we based our inferences on population size on the unweighted average of the estimates from models 3 and 4.

In Fig. 4 we compare these model-averaged estimates with those under model 2, which corrects for random rather than nonrandom coverage bias (i.e., this model assumes  $\kappa = 0$ ), and with the observed number of counted pairs. We see substantial differences in the trend estimates under the PS models relative to the observed data, especially during the earlier years. We also see that PS-naïve imputation of site occupancy in model 2 led to serious overestimates of population size during the earlier years and to trend estimates that were too strongly negative. Based on the model-averaged estimates, the sizes of all but one regional subpopulation peaked between 2002

and 2007 (Tab. 3). In the French and the Swiss Jura, peaks occurred in 2000 and 2007, respectively. The population in the Jura as a whole peaked in 2007 at an estimated 303 pairs, which translated into a range-wide average density of 1.86 pairs/100 km<sup>2</sup>. A comparison between the estimated population size in the peak year and that in 2020 revealed declines that ranged from 5% in the Dép Ain to 38% in the Jura Nord and a Jura mountain-wide decline of 9 % from 2007 to 2020 (CRI 6–12; see Tab. 3). For only one region (Jura Sud) did we estimate an increase, but we point out again that the comparability of the data before and after 2017/2018 seems doubtful (see above).

As an alternative measure of population change, we fit a simple linear regression through the model-averaged population size estimates, to characterize the change not just based on two years (i.e., the peak year and the final year of 2020), but on all the years between 2000 and 2020 (or 2005 and 2020 in the case of the Jura Nord). Inspection of the posterior distributions of the slope parameters showed significant population declines in every single region, in the French and Swiss Jura, and the Jura mountains as a whole (Tab. 4, left). For all eight analyses, the probability of a population decline was estimated >0.99. These negative slope estimates have the neat interpretation of an average annual number of Peregrine pairs lost between 2000 and 2020. The annual loss to the population ranged between 0.12 in the Jura Sud and 0.85 in the Jura Nord. Overall, 2.13 pairs were estimated to be lost in the Jura mountains in every single year between 2000 and 2020.

These trend assessments differed sharply from inferences under simple linear regressions fit through the *observed* counts of pairs, i.e., without any correction for the coverage bias (Tab. 4, right). With the *observed* counts of pairs, the only significant decline was found in the Dép Jura, while a significant increase, rather than a decline, was diagnosed for the whole Jura mountains, highlighting the biasing effects of uncorrected coverage bias.

## DISCUSSION

We used occupancy modeling to identify the years of peak recovery and assess spatiotemporal variation in post-recovery population trends in a large Western European population of Peregrine falcons in the Jura mountains from 2000–2020, and to infer rates of site persistence and site colonization. We put particular emphasis on the twin issues of the correction for coverage bias and on preferential sampling as a nonrandom form of coverage bias. The population peaked in different regions between 2000 and 2007, and in 2007 in the Jura mountains as a whole with an estimated 303 pairs. Post-peak trends were negative in four regions, with as much as a 38%

decline over only about a decade in the Swiss Jura Nord. Dynamic occupancy modeling enabled estimation of site persistence and colonization probabilities, which are the demographic causes of population change at the level of a site. We found considerable spatiotemporal variation in both parameters, with the most striking result being a major drop in the Jura Nord, thus mirroring the strong population decline in that region. Ignoring coverage bias caused by nonvisitation of some sites would have underestimated population sizes substantially and would have led us to diagnose erroneous trends, including an increase rather than a decline in the Jura mountains as a whole. This emphasizes the importance of correcting for coverage bias in population studies in the common case where all sites cannot be surveyed in every year.

We found that post-recovery trends were highly variable in space at a scale of less than few 100 km. One region (Jura Nord) showed a particularly severe decline of 38% over less than 10 years, and in contrast, the adjacent Swiss region (Jura Sud) showed a much weaker decline or possibly even an increase (although the latter may be doubtful because of methodological changes after 2017/2018). It is natural to wonder about likely causes of the declines and the regional variation in the rate of these declines. Circumstantial evidence suggests multiple, natural and "unnatural" causes, including increasing predation by a main predator of the Peregrine, the European Eagle owl (*Bubo bubo*), illegal persecution, human disturbance, and perhaps also delayed density-dependence. In contrast, we believe that we can rule out increased spring precipitation (Carlzon *et al.* 2018, Zuberogitia *et al.* 2018) or declines in the prey base. We discuss each of these in turn.

Up to about the 1970s, the eagle owl had been extinct in most of the Jura mountains for many decades due to human persecution (LPO Franche-Comte 2018). Since then, it has made an impressive comeback with colonization likely coming both from the major, expanding populations in the Southwest (i.e., from France) and the North-East (i.e., from Germany). Many former Peregrine sites have been taken over by Eagle owls, and while in some cases the Peregrines simply moved to adjacent sites (e.g., 1 km away or more), there were others where a Peregrine site was eclipsed by the colonization of an eagle owl (Monneret 2010, and authors' unpublished observations). Predation by eagle owls is the major one among the hypothesized factors that acts range-wide in the Jura that may have caused at least partly the observed declines (Brambilla *et al.* 2006, Lindner 2018). Moreover, within Switzerland it seems that the Eagle owl is so far inexplicably much scarcer in the Jura Sud than in the Jura Nord, where it has become fairly widespread (Knaus *et al.* 2018, and unpublished field data) and has taken over a substantial

number of former Peregrine sites. This observation is consistent with much more severe declines of the Peregrine in the Jura Nord than in the Jura Sud.

Like many other raptors, Peregrines have probably always been persecuted despite decades of legal protection in France and Switzerland. It appears that poisoning with baited prey such as so-called "kamikaze pigeons" deployed by reckless pigeon fanciers is the recent method of choice in many areas. In Switzerland, in recent years information has been collated on more than 30 proven or suspected cases of the poisoning of Peregrines typically with baited pigeons (Inderwildi *et al.* 2018, Martin Sinniger, pers. comm.). Interestingly, the only Jura region where this sort of illegal persecution has become known is around the Northern and Eastern fringe of the Jura Nord. This may not mean much, because there are so many unknowns involved, but nevertheless we know from Altwegg *et al.* (2014) that in a small Peregrine study population of about 20 pairs, annual immigration of as few as 0–2 individuals made all the difference between a strongly increasing population and a stable or even slightly declining population. In analogy we might surmise that in the Jura Nord, with a population that is 2-4 times bigger, 2–8 killed birds annually might make the difference between a stable population and one that is in a fairly steep decline, as observed.

Finally, as in many other regions, Peregrine sites are outdoor magnets for humans and their many activities including rock climbing, sightseeing, geo-caching, delta- and paragliding, caving or bird photography, all of which may disturb the adults and thereby indirectly destroy Peregrine broods (Brambilla *et al.* 2004). Problems are expected to be greater when cliffs are smaller and people more plentiful. In this respect, the Peregrines in the Jura Nord appear again more vulnerable, since the cliffs in this region are often smaller than in the other regions and, especially, this region has a higher human population density and is closer to major population centres than the other regions of the Jura mountains.

Finally, we may hypothesize that a natural cause may also be involved in post-peak declines: delayed density dependence. If density dependence acts more severely on the survival of young birds but it takes a couple of years until they become recruited into the breeding part of the population, then a recovering population regulated by density dependence will tend to "overshoot" some at first (Hornfeldt 1994, Hansen *et al.* 1996, Ergon *et al.* 2011). In line with possible density dependence in first-year Peregrines, declines in survival were recently found for them, but not for adults in the recovering British population (Robinson & Wilson 2021, although see also Smith *et al.* 2015).

In contrast, changes in spring precipitation as found by Zuberogitia *et al.* (2018) in the Basque country do not appear to be a suitable candidate for explaining the recent declines. We tested whether there was any increase in annual precipitation sums in the Swiss Jura Nord, where the population decline was most pronounced, and found no trends in February, April and May, and a decrease in March (unpublished analysis). In addition, there is no evidence for recent reductions in the Peregrine prey base; quite on the contrary, the recently published Swiss breeding bird atlas (Knaus *et al.* 2018) shows stable or increasing populations for most of the major prey species such as finches, starling, thrushes and pigeons between the mid-1990s and now.

Clearly, this is only a first attempt at assessing different causal hypotheses about the recent declines observed in the Jura, and more work will be needed to discriminate among them. For instance, Peregrine declines due to predation by the recovering Eagle owl population might simply be due to the natural effects of a top- on a meso-predator (e.g., Newsome *et al.* 2017). Increased predation from eagle owls and delayed density-dependence both reflect the restoration of natural population limitation, while persecution and disturbance are unnatural if we follow the notion that humans are outside of the natural world. Thus, elucidation of the relative effects of these hypothesized causes will be important to decisions about whether and which conservation measures are needed to reverse these recent declines.

In our study there was a clear and strong need to impute missing values caused by missing site visits, in order to correct population size estimates for coverage bias. Under a given model, this can be done very easily, and with full error propagation, in a Bayesian analysis conducted with the usual simulation techniques, i.e., MCMC (Gelman *et al.* 2003). However, unless sites are visited randomly, it will be crucial to accommodate the type of selection bias that will usually lead observers to visit "better" sites first. This selection bias may be conscious or even prescribed in the protocol of a survey, or it may be unconscious. But it is very likely there and the result is PS (Diggle *et al.* 2010, Pacifici *et al.* 2012, 2016, Conn *et al.* 2017, Monneret *et al.* 2018, Fandos *et al.* 2021) and if this type of nonrandom coverage bias is not accounted for, then biased assessments of population status and trends may result. Therefore, in many citizen-science population studies, it may be crucial to test for deviations from random sampling of the site visitation patterns and if PS is found, correct for it in a joint model of the kind described in the cited papers and shown in our study as well. Our understanding of PS is still in its infancy though and we need more empirical and also simulation studies that may shed light on how to best model it in each case. In our study (as also in Monneret *et al.* 2018) we chose two formulations of PS that appeared reasonable to us

and that may span a range of psychological mechanisms underlying PS, i.e., a long- and a short-term dependence of visitation on perceived site quality. Inferences under the two models with PS were fairly similar in our case (not shown) and hence, we think that our reported results accounting for PS are probably robust.

It is worth pointing out that as an alternative to the model-based solution to PS, one might also choose design-based alternatives and simply visit all sites in each year, an annually varying fraction or a constant sample of all sites. In all three cases there would no longer be any connection between site quality and the incidence of missing values and thus a simpler imputation method could be used for the latter two cases. However, there are also costs to these. Identifying the most efficient survey design that represents the best tradeoff between survey costs, information quantity and model complexity is best tackled by a simulation study, and the optimum solution is almost bound to vary to some degree from case to case.

Like most population studies unfortunately we did not account for imperfect detection of occupied sites, even though we did use an occupancy model for inference, albeit one without a submodel for the observation process. This is quite unfortunate, especially since the required replicate visits are in fact conducted at most surveyed sites; only, we don't know their results, since only the aggregate results over all surveys at a site within a breeding season is recorded. However, in our case, a majority of sites are visited repeatedly within a season and thus the combined detection probability of a pair will be fairly high. Thus, we think it is extremely unlikely that the strong spatio-temporal patterns in the observed number of occupied sites would be a mere artifact of similar patterns in detection probability (although we cannot prove this). At any rate, recording separate results for every site visit would greatly strengthen the inferences from any population study such as ours.

Our finding of some severe post-recovery declines in a Peregrine population are not entirely unique. For instance, a recent trend assessment in Great Britain has identified declines of Peregrines in several regions as well (Wilson *et al.* 2018) as has a study in the Basque country (Zuberogoitia *et al.* 2018). Nevertheless, such findings are still relatively rare in the worldwide success story of this species and similar former pesticide victims. We think that it is important that they are documented, because they show that the situation of a species that was believed to be out of danger may be reversed in very little time, at least regionally, and this is an important message for conservation.

Our study has showcased the power of occupancy models to estimate population size and make inferences about the site-level population dynamics parameters that underlie population

changes (MacKenzie et al. 2012, chapters 4 and 6 in Kéry & Royle, 2021). One of the main advantages of an occupancy model over an individual-level demographic model such as a matrix model (Caswell, 2001) or an integrated population model (Besbeas *et al.* 2002, Schaub & Kéry, 2021) is that it can be fit to "cheaper" and much more widely available data: site-occupancy data, without any need for marking animals. It is highly likely that the site-level dynamics rates, i.e., colonization and persistence probability, will reflect to some degree also the individual-level demographics, i.e., apparent survival and recruitment. However, the relationship is not direct, although some exciting attempts at formalizing it have been made (Roth & Amrhein 2010, section 4.12 in Kéry & Royle 2021). But we would like to emphasize that we do not think that a site-occupancy-based analysis of population demographics can ever make obsolete a deeper, individual-level demographic study based on data from marked individuals.

This study would not have been possible without the dedicated efforts of a large number of volunteer Peregrine researchers over many decades. Indeed, we believe that the value of long-term population studies such as the three surveys that we combined in our analysis can hardly be overstated, especially in a time when we see mass-participation citizen-science programs mushrooming all over the world. We are convinced that targeted surveys in a study that has at least some structured protocol (for instance, by distinguishing a Peregrine site from a nonsite and encouraging multiple visits of each in every spring) produce *much* more reliable data for assessments of population status and trends in many species, and especially those with large territories such as many raptors. Thus, the deceiving allure of Big Data should not conduce us to think that targeted population surveys may become obsolete any time soon. Nevertheless, ways should be found to optimize targeted surveys such as ours, for instance, by keeping records from individual site visits separate such that observation errors (i.e., imperfect detection and possibly false positives) can be formally corrected for in a full occupancy modeling framework (MacKenzie *et al.* 2017, Kéry & Royle 2016, 2021).

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Name	French Département Ain (01)	French Département Jura (39)	French Département Doubs (25)	Swiss Jura Sud	Swiss Jura Nord
Dép Ain	<b>X</b>	-	-	-	-
Dép Jura	-	<b>X</b>	-	-	-
Dép Doubs	-	-	<b>X</b>	-	-
Jura Sud	-	-	-	<b>X</b>	-
Jura Nord	-	-	-	-	<b>X</b>
French Jura	<b>X</b>	<b>X</b>	<b>X</b>	-	-
Swiss Jura	-	-	-	<b>X</b>	<b>X</b>
Jura mountains	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>

Table 1: Explanation of the names for the geographic entities in this article, see also Fig. 1

Region	Model 3 (long-term PS)		Model 4 (immediate effect of PS)	
	$\kappa$	CRI	$\kappa$	CRI
Dép Ain	1.41	1.16, 1.69	2.76	2.39, 3.12
Dép Jura	1.33	1.08, 1.64	2.89	2.36, 3.44
Dép Doubs	1.08	0.91, 1.27	2.93	2.59, 3.28
Jura Sud	1.11	0.91, 1.27	3.28	2.77, 3.84
Jura Nord	0.23	0.17, 0.30	0.95	0.71, 1.20

Table 2: Estimates (posterior means and 95% CRIs) of the coefficient  $\kappa$  (kappa) representing the strength of preferential sampling (PS) under a model with an effect of long-term perceived site quality (model 3; left) and one with an immediate effect of perceived site quality (model 4; right); see Methods for further explanation on these two models. Note that  $\kappa = 0$  would denote random visitation of sites.

Geographic Stratum (Region)	Peak year	Change until 2020 (posterior mean)	95% CRI
Dép Ain	2007	- 5%	- 12%, + 1%
Dép Jura	2002	- 8%	- 14%, - 3%
Dép Doubs	2005	- 9%	- 14%, - 4%
<i>Jura Sud*</i>	2020	+ 11%	+ 7%, + 12%
Jura Nord	2007	- 38%	- 41%, - 34%
French Jura	2000	- 4%	- 10%, +3%
Swiss Jura	2007	- 21%	- 25%, - 18%
Jura mountains	2007	- 9%	- 12%, -6%

Table 3: Total change of population size (in %) between the peak year and the last year of study (2020) based on the model-averaged estimates from models 3 and 4 which both account for preferential sampling. (\* see Methods for limitations in the comparability of results before and after 2017/2018 in this region).

Stratum, region	Average of models 3 and 4 (with PS correction)			Observed counts		
	Slope	CRI	Prob. of decline	Slope	CRI	Prob. of decline
Dép Ain	- 0.24	- 0.46, - 0.05	<b>&gt;0.99</b>	0.27	- 0.22, 0.77	0.13
Dép Jura	- 0.50	- 0.63, - 0.39	<b>&gt;0.99</b>	- 0.29	- 0.55, -0.03	<b>0.98</b>
Dép Doubs	- 0.35	- 0.61, - 0.12	<b>&gt;0.99</b>	0.47	- 0.05, 1.02	<b>0.04</b>
<i>Jura Sud*</i>	- 0.12	- 0.21, - 0.03	<b>&gt;0.99</b>	- 0.08	- 0.33, 0.18	0.27
Jura Nord	- 0.85	- 1.34, - 0.33	<b>&gt;0.99</b>	- 0.74	- 1.81, 0.46	0.91
French Jura	- 1.12	- 1.63, - 0.67	<b>&gt;0.99</b>	0.78	- 0.12, 1.85	0.05
Swiss Jura	- 1.01	- 1.53, - 0.47	<b>&gt;0.99</b>	1.38	- 0.15, 3.01	<b>0.04</b>
Jura mountains	- 2.13	- 3.08, - 1.22	<b>&gt;0.99</b>	6.44	2.59, 12.12	<b>0.00</b>

Table 4: Left: Estimates of the slopes of linear regressions fit through the model-averaged estimates from models 3 and 4 of population size in different regions/strata of the Jura mountains, and for the Jura as a whole, between 2000–2020 (only 2005–2020 in the Jura Nord). Right: analogous estimates from linear regressions through the observed number of pairs. In this analysis these slopes can be interpreted as the average annual change in the number of Peregrine pairs during that period. Posterior means and 95% CRIs are given, and significant trends (declines or increases) are shown in bold face. (\* see Methods for limitations in the comparability of results before and after 2017/2018 in this region)

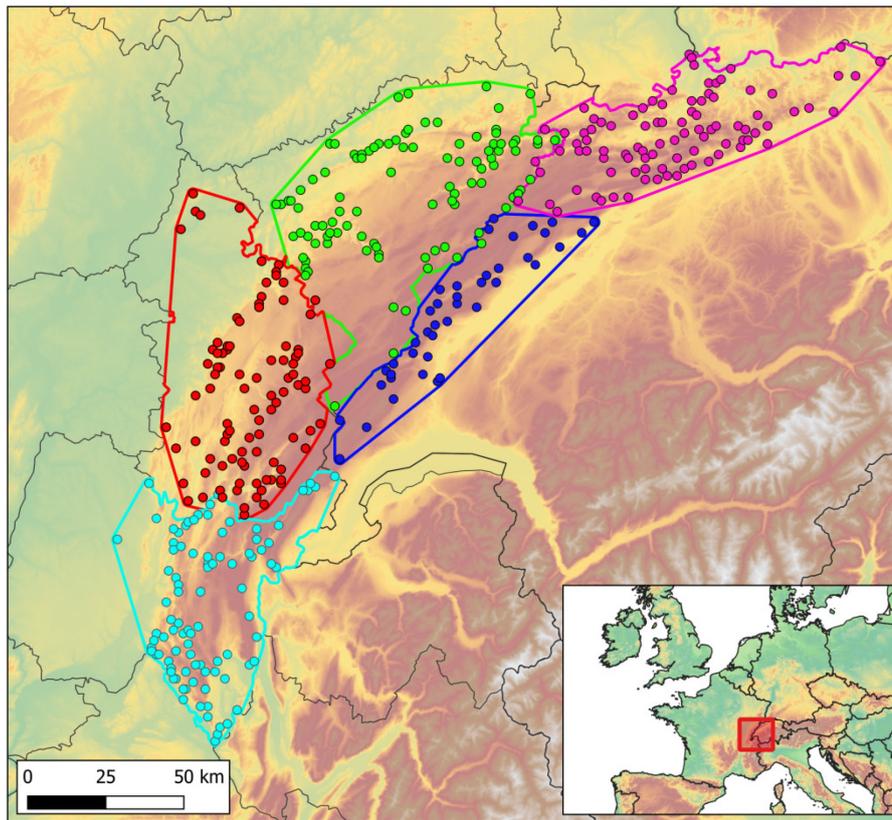


Fig. 1: Distribution of the 420 Peregrine breeding sites known in the Jura mountains (16,304 km<sup>2</sup>), showing the stratification by three political Departments on the French side and two surveys schemes on the Swiss side. Three strata on the French side of the Jura mountains are the Départements Ain (lightblue), Jura (red) and Doubs (green), and two strata are on the Swiss side of the Jura: Jura Sud (dark blue) and Jura Nord (magenta). A Peregrine breeding site was defined by the observation of a Peregrine pair at a potential nesting site at least once during the breeding season of the years 1960–2020 (and most sites had also confirmed breeding); note that not all of those sites were simultaneously occupied.

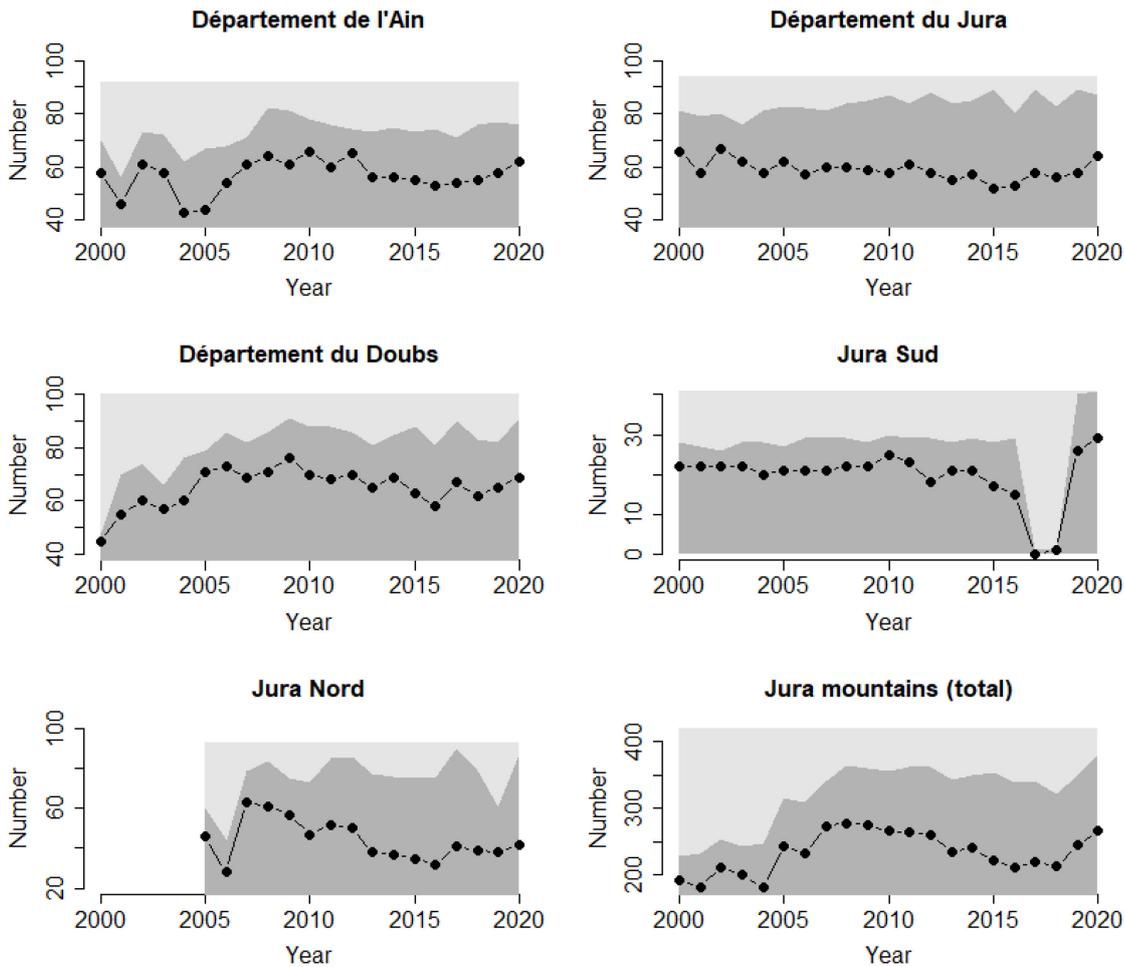


Fig. 2: Annual number of surveyed sites (dark polygons) in the five regions (and the rangewide total at the bottom right) in the Jura mountains and the observed annual number of pairs ("raw population size"; black circles). Light grey polygons show the number of known sites that were not surveyed in each year. A main aim of any population size assessment must be to "fill in" the unknown occupancy state for the light-grey (i.e., the unsurveyed) sites.

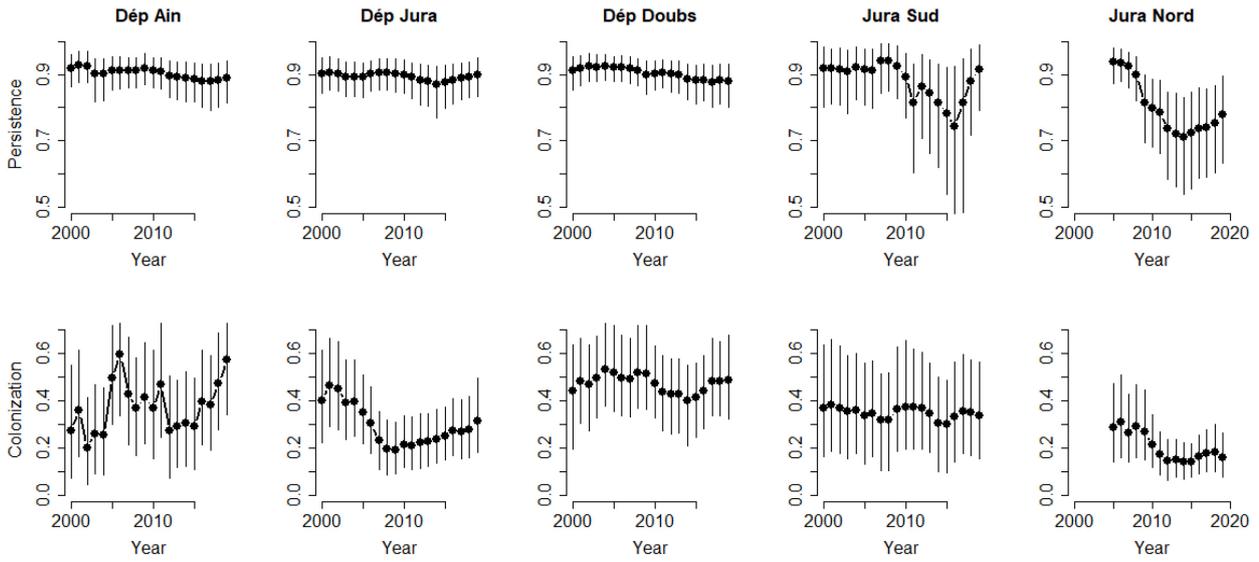


Fig. 3: Estimates of site persistence (top) and site colonization rates (bottom) between 2000 and 2020 for the five regions distinguished in the Jura mountains under model 1. Posterior means and 95% CRIs are shown. The latter convey the uncertainty due to our correction for coverage bias, but ignore effects of possible non-detection bias.

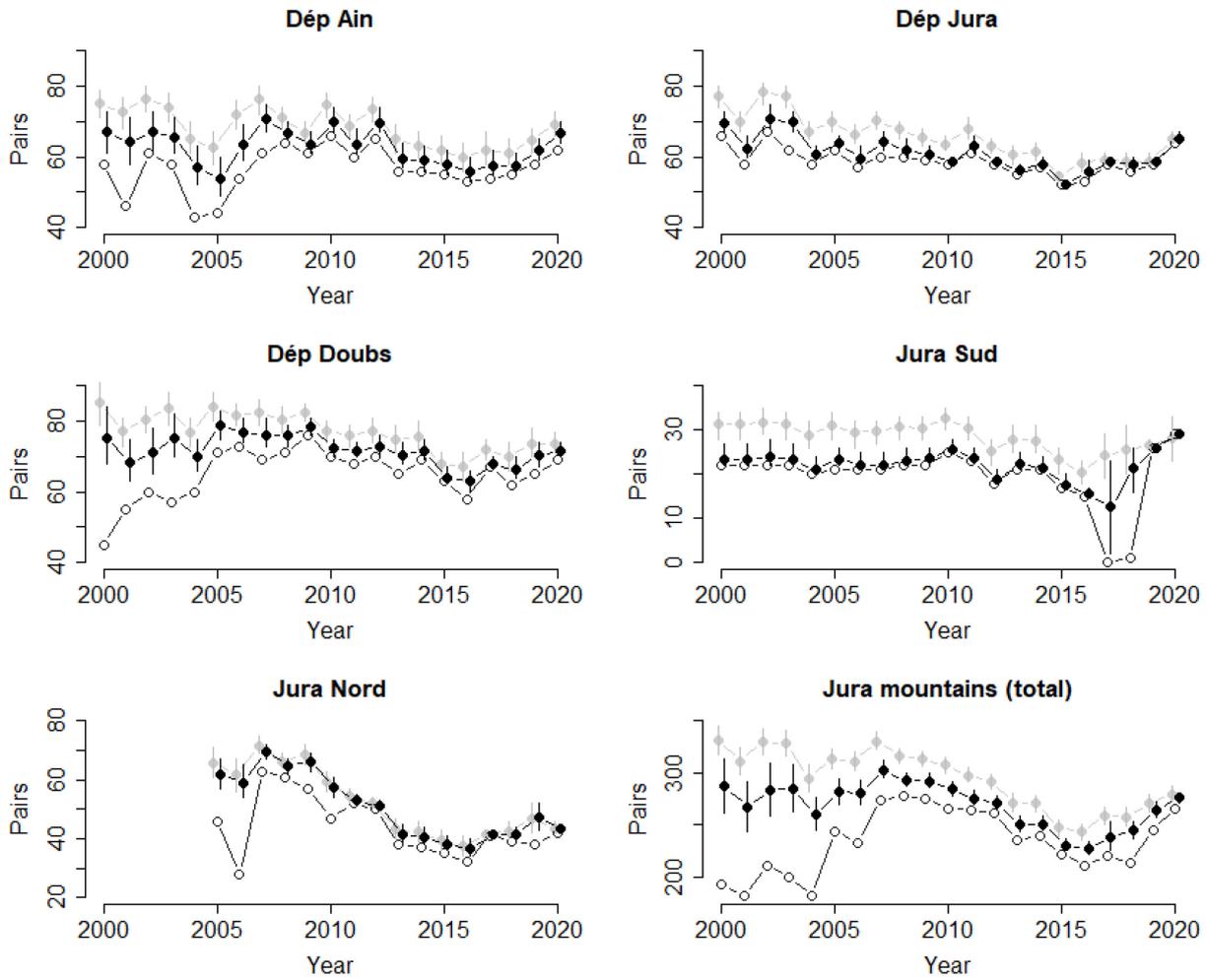


Fig. 4: Observed and estimated trajectories of population size (number of pairs) of the Peregrine falcon in the five regions in the Jura mountains, and for the Jura mountains as a whole. We contrast the "raw population size", i.e., the observed total number of territorial pairs (open symbols) and the estimates under model 2 that accounts for site heterogeneity and corrects for *random* coverage bias (grey symbols) and the model-averaged estimates under models 3 and 4, which account for non-random (i.e., preferential) coverage bias (black symbols). Model output is given as posterior means and 95% CRIs, where the latter show the uncertainty due correction for coverage bias, but ignore possible nondetection bias.

## APPENDIX: FORMULATIONS OF THE FOUR MODELS FIT IN THIS STUDY IN THE BUGS LANGUAGE AS IMPLEMENTED IN JAGS.

**Model 1:** This is a dynamic occupancy model with separate random-walk smoothers for time in persistence and colonization probability.

### # Specify model in BUGS language

```
cat(file = "modell.txt", "  
model {
```

### # Priors and models for parameters

```
for(k in 1:5){  
  psi1[k] ~ dbeta(1, 1)      # Initial occupancy depends on region  
}
```

### # Model for phi and gamma: region + random site effects + smooth random year effects

```
for (i in 1:nsites){  
  for(t in 1:(nyears-1)){  
    logit(phi[i,t]) <- lphi[i,t]  
    lphi[i,t] <- lphi.site[i] + lphi.year[region[i],t]  
    logit(gamma[i,t]) <- lgamma[i,t]  
    lgamma[i, t] <- lgamma.site[i] + lgamma.year[region[i],t]  
  }  
  lphi.site[i] ~ dnorm(alpha.lphi[region[i]], tau.lphi.site)  
  lgamma.site[i] ~ dnorm(alpha.lgamma[region[i]], tau.lgamma.site)  
}
```

### # Priors for region-specific phi and gamma intercepts

```
for(k in 1:5){      # Loop over the 5 geographical strata  
  alpha.lphi[k] <- logit(initial.phi[k])  
  initial.phi[k] ~ dbeta(1, 1)  
  alpha.lgamma[k] <- logit(initial.gamma[k])  
  initial.gamma[k] ~ dbeta(1, 1)  
}  
tau.lphi.site <- pow(sd.lphi.site, -2)  
sd.lphi.site ~ dunif(0, 5)  
tau.lgamma.site <- pow(sd.lgamma.site, -2)  
sd.lgamma.site ~ dunif(0, 5)
```

### # Priors for year effects on phi and gamma with rw smoothers

### # Now we make all smoothers differ by region

```
for(k in 1:5){      # Loop over the 5 geographical strata  
  lphi.year[k,1] <- 0  # Set to zero to avoid overparameterization  
  lgamma.year[k,1] <- 0  
  for (t in 2:(nyears-1)){  
    lphi.year[k,t] ~ dnorm(lphi.year[k,t-1], tau.eps.lphi[k])  
    lgamma.year[k,t] ~ dnorm(lgamma.year[k,t-1], tau.eps.lgamma[k])  
  }  
  tau.eps.lphi[k] <- pow(sd.eps.lphi[k],-2)  # Hyperpriors for variances  
  sd.eps.lphi[k] ~ dunif(0, 2)  
  tau.eps.lgamma[k] <- pow(sd.eps.lgamma[k],-2)  
  sd.eps.lgamma[k] ~ dunif(0, 2)  
}
```

### # Ecological and observation submodels confounded (no p)

```

for (i in 1:nsites){
  y[i,1] ~ dbern(psil[region[i]])
  for (t in 2:nyears){
    y[i,t] ~ dbern(y[i,t-1]*phi[i,t-1] + (1-y[i,t-1])*gamma[i,t-1])
  }
}

# Derived parameters
# Population occupancy and population size
n.occ[1] <- sum(y[1:nsites,1])
for (t in 2:nyears){
  n.occ[t] <- sum(y[1:nsites,t])      # Number of occupied sites
}
# Year-specific average values of phi and gamma
for(t in 1:(nyears-1)){
  mean.phi.year[t] <- mean(phi[,t])
  mean.gamma.year[t] <- mean(gamma[,t])
}

# Region- and year-specific averages of phi and gamma
# Averaged over sites
for (k in 1:5){
  for(t in 1:(nyears-1)){
    phi.region.year[k,t] <- ilogit(alpha.lphi[k] + lphi.year[k,t] )
    gamma.region.year[k,t] <- ilogit(alpha.lgamma[k] + lgamma.year[k,t])
  }
}

# Average gamma and phi per region in the central year (2010)
for(k in 1:5){
  logit(gamma.region[k]) <- alpha.lgamma[k] + lgamma.year[k, 11]
  logit(phi.region[k]) <- alpha.lphi[k] + lphi.year[k, 11]
}

# Population size in each region
for (t in 1:nyears){
  n.ain[t] <- sum(y[1:95, t])
  n.jura[t] <- sum(y[96:191, t])
  n.doubs[t] <- sum(y[192:292, t])
  n.JuraS[t] <- sum(y[293:333, t])
  n.JuraN[t] <- sum(y[334:426, t])
}
}
")

```

**Model 2:** This is a static, multi-year occupancy model with a random-walk smoother on occupancy probability.

```

# Specify model in BUGS language
cat(file = "model2.txt", "
model {

# (Only) Submodel: model results of surveys
#-----
# Specify priors and constraints
for (i in 1:nsites){
  for (t in 1:nyears){
    logit(psi[i,t]) <- alpha[region[i]] + eps.year[t]
  } #t
} #i
for (k in 1:5){
  alpha[k] <- logit(psi.int[k])
  psi.int[k] ~ dunif(0, 1)
}

# Correlated year effects (random-walk smoother)
# eps.year[1] ~ dnorm(0, 0.1)
eps.year[1] <- 0 # Need this to avoid overparameterization !
for(t in 1:(nyears-1)){
  eps.year[t+1] <- eps.year[t] + diff.eps.year[t]
  diff.eps.year[t] ~ dnorm(0, tau.diff.eps.year)
}
tau.diff.eps.year <- pow(sd.diff.eps.year, -2)
sd.diff.eps.year ~ dunif(0, 1)

# Ecological submodel (no observation model)
for (i in 1:nsites){
  for (t in 1:nyears){
    y[i,t] ~ dbern(psi[i,t])
  } #t
} #i

# Derived parameters: Various population sizes
for (t in 1:nyears){
  # Total population size in the Arc jurassien
  n.occ[t] <- sum(y[,t])
  # Population sizes in French and Swiss parts of the Jura
  n.F[t] <- sum(y[1:292,t])
  n.CH[t] <- sum(y[293:426,t])
  # Population sizes in each region
  n.ain[t] <- sum(y[1:95, t])
  n.jura[t] <- sum(y[96:191, t])
  n.doubs[t] <- sum(y[192:292, t])
  n.JuraS[t] <- sum(y[293:333, t])
  n.JuraN[t] <- sum(y[334:426, t])
}
}
")

```

**Model 3:** This is static, multi-year occupancy model with a random-walk smoother on occupancy probability and with a formulation of preferential sampling that links site occupancy and site visitation through random site effects in the former that are used as predictors for site visitation probability in the latter.

```

# Specify model in BUGS language
cat(file = "model3.txt", "
model {

# Submodel 1: model results of surveys
#-----
# Specify priors and constraints
for (i in 1:nsites){
  for (t in 1:nyears){
    logit(psi[i,t]) <- alpha[i] + eps.year[t]
  }
  alpha[i] ~ dnorm(mu.lpsi.region[region[i]], tau.lpsi.site)

  # Compute region-centered site effect as a site quality trait
  eps.site[i] <- alpha[i] - mu.lpsi.region[region[i]]
}

for (k in 1:5){
  mu.lpsi.region[k] <- logit(mean.psi.region[k])
  mean.psi.region[k] ~ dunif(0, 1)
}
tau.lpsi.site <- pow(sd.lpsi.site, -2)
sd.lpsi.site ~ dunif(0, 5)

# Correlated year effects (random-walk smoother)
eps.year[1] <- 0 # Need this to avoid overparameterization !
for(t in 1:(nyears-1)){
  eps.year[t+1] <- eps.year[t] + diff.eps.year[t]
  diff.eps.year[t] ~ dnorm(0, tau.diff.eps.year)
}
tau.diff.eps.year <- pow(sd.diff.eps.year, -2)
sd.diff.eps.year ~ dunif(0, 1)

# Ecological submodel (no observation model)
for (i in 1:nsites){
  for (t in 1:nyears){
    y[i,t] ~ dbern(psi[i,t])
  }
}

# Derived parameters: Various population sizes
for (t in 1:nyears){
  # Total population size in the Arc jurassien
  n.occ[t] <- sum(y[,t])
  # Population sizes in French and Swiss parts of the Jura
  n.F[t] <- sum(y[1:292,t])
  n.CH[t] <- sum(y[293:426,t])
  # Population sizes in each region
  n.ain[t] <- sum(y[1:95, t])
  n.jura[t] <- sum(y[96:191, t])
  n.doubs[t] <- sum(y[192:292, t])
  n.JuraS[t] <- sum(y[293:333, t])
}

```

```

n.JuraN[t] <- sum(y[334:426, t])
}

# Submodel 2: model whether a site is visited or not
# -----
# Model for theta: ~ region + region:PS + year + year^2
# Specify priors and constraints
for (i in 1:nsites){
  for (t in 1:nyears){
    logit(theta[i,t]) <- alpha.visit[region[i]] +
      kappa[region[i]] * eps.site[i] +
      beta.visit[1] * year[t] + beta.visit[2] * pow(year[t],2)
  }
}
for(k in 1:5){
  alpha.visit[k] <- logit(theta.int[k])
  theta.int[k] ~ dunif(0, 1)
  # Half-normal prior with non-negative mass
  kappa[k] ~ dnorm(0, 0.1)I(0, )
}

for(v in 1:2){
  # Only up to quadratic now
  beta.visit[v] ~ dnorm(0, 0.1)
}

# Bernoulli model for visits (R)
for (i in 1:nsites){
  for (t in 1:nyears){
    R[i,t] ~ dbern(theta[i,t])
  }
}
}
")

```

**Model 4:** A static, multi-year occupancy model with a random-walk smoother on occupancy probability and with a formulation of preferential sampling that links site occupancy and site visitation through the partially latent presence/absence state of a site that is used as a predictor for site visitation probability.

```

# Specify model in BUGS language
cat(file = "model4.txt", "
model {

# Submodel 1: model results of surveys
#-----
# Specify priors and constraints
for (i in 1:nsites){
  for (t in 1:nyears){
    logit(psi[i,t]) <- alpha[i] + eps.year[t]
  }
  alpha[i] ~ dnorm(mu.lpsi.region[region[i]], tau.lpsi.site)

# Compute region-centered site effect as a site quality trait
eps.site[i] <- alpha[i] - mu.lpsi.region[region[i]]
}

for (k in 1:5){
  mu.lpsi.region[k] <- logit(mean.psi.region[k])
  mean.psi.region[k] ~ dunif(0, 1)
}
tau.lpsi.site <- pow(sd.lpsi.site, -2)
sd.lpsi.site ~ dunif(0, 5)

# Correlated year effects (random-walk smoother)
eps.year[1] <- 0 # Need this to avoid overparameterization !
for(t in 1:(nyears-1)){
  eps.year[t+1] <- eps.year[t] + diff.eps.year[t]
  diff.eps.year[t] ~ dnorm(0, tau.diff.eps.year)
}
tau.diff.eps.year <- pow(sd.diff.eps.year, -2)
sd.diff.eps.year ~ dunif(0, 1)

# Ecological submodel (no observation model)
for (i in 1:nsites){
  for (t in 1:nyears){
    y[i,t] ~ dbern(psi[i,t])
  }
}

# Derived parameters: Various population sizes
for (t in 1:nyears){
  # Total population size in the Arc jurassien
  n.occ[t] <- sum(y[,t])
  # Population sizes in French and Swiss parts of the Jura
  n.F[t] <- sum(y[1:292,t])
  n.CH[t] <- sum(y[293:426,t])
  # Population sizes in each region
  n.ain[t] <- sum(y[1:95, t])
  n.jura[t] <- sum(y[96:191, t])
  n.doubs[t] <- sum(y[192:292, t])
  n.JuraS[t] <- sum(y[293:333, t])
}

```

```

n.JuraN[t] <- sum(y[334:426, t])
}

# Submodel 2: model whether a site is visited or not
# -----
# Model for theta: ~ region + region:PS + year + year^2
# Specify priors and constraints

# Year 1: no effect of immediate behavioural response (IBR)
for (i in 1:nsites){
  logit(theta[i,1]) <- alpha.visit[region[i]] +
    beta.visit[1] * year[1] + beta.visit[2] * pow(year[1],2)
}

# Year 2:nyear: including an IBR
for (i in 1:nsites){
  for (t in 2:nyears){
    logit(theta[i,t]) <- alpha.visit[region[i]] +
      kappa[region[i]] * y[i, (t-1)] +
      beta.visit[1] * year[t] + beta.visit[2] * pow(year[t],2)
  }
}
for(k in 1:5){
  alpha.visit[k] <- logit(theta.int[k])
  theta.int[k] ~ dunif(0, 1)
  # Half-normal prior with non-negative mass (or uniform)
  kappa[k] ~ dunif(0, 10)
}

for(v in 1:2){
  # Only up to quadratic now
  beta.visit[v] ~ dnorm(0, 0.1)
}

# Bernoulli model for visits (R)
for (i in 1:nsites){
  for (t in 1:nyears){
    R[i,t] ~ dbern(theta[i,t])
  }
}
}
")

```