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The Peregrine population study in the French Jura mountains 1964–2016: use of occupancy modeling to estimate population size and analyze site persistence and colonization rates

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Summary We summarize key results of the first 53 years of one of the longest-running avian population studies in the world, on the Peregrine Falcon *(Falco peregrinus),* in the French Jura mountains (12,714 km^2), launched in 1964. A total of 449 cliff sites in 338 potential Peregrine territories were surveyed: 287 (85%) of these territories were occupied by an adult pair at least once, while in 51 (15%) we never detected an adult pair. Most sites were visited several times during a breeding season to survey occupancy and later fecundity, but the proportion of sites visited was highly variable over the years. We highlight the power of the Bayesian implementation of site-occupancy models (MacKenzie *et al.* 2002, 2003) to analyze data from raptor population studies: to correct population size estimates for sites not visited in a given year and for the biasing effects of preferential sampling (when better sites are more likely to be checked). In addition, these models allow estimation and modeling of the site-level persistence and colonization rates, which can provide important clues about drivers of population dynamics, even without individually marking any birds. Changes in the dynamics rates may serve as early-warning signals for subsequent population declines.

Since 1964, the observed number of adult pairs varied between 17 in 1972 and 196 in 2008, but the proportion of sites visited increased from 43% in 1964 to 80–90% after 2002. Hence, this raw population total must be an underestimate. We found strong evidence for preferential sampling in our study. Correcting for this, we estimated 56 pairs in 1964, after which the population dropped to a minimum of 18 in 1972, but then recovered rapidly, leveling off somewhat around 1995 and reaching a maximum of 200–210 adult pairs during 2000–2012. This was then followed by a decline to 170–190 pairs. In any one year, the raw counts underestimated the true population size by 5–39% (mean 11%), due to sites not being visited (this correction ignores imperfect detection though). Site persistence rates declined from 78% to less than 60% during 1967–1972, and then increased rapidly to over 90% during 1980–1990, suggesting that once pesticide effects vanished, individual survival probability increased rapidly and as a consequence also site persistence. Since the 1990s, persistence has declined slowly, which may indicate decreasing adult survival. In contrast, colonization rates increased steadily from about 3% in the early years to maxima of 46–49% during 1994–2001, but declined thereafter and currently reach about 33%. Taller cliffs had greater persistence and colonization rates than medium or small cliffs.

Both the decline in colonization and in persistence rates during the last 15 years may reflect density-dependence, predation by the expanding European Eagle Owl *(Bubo bubo)* population, human persecution or any as yet unknown factors. Importantly, we note that both persistence and colonization rates began to decline many years before the recent population decline became apparent. Thus, analysis of population studies using dynamic occupancy models can provide early-warning signals for future population declines. Our study demonstrates the benefits of modern analytical methods that can correct for several key deficiencies in probably all raptor population studies: incomplete coverage of sites and imperfect detection (though we only dealt with the former here). Occupancy models, possibly accounting for preferential sampling, appear to represent the logical analytical framework for abundance in raptor population studies.

Keywords: Bayesian, BUGS, Dynamic occupancy model, colonization, detection probability, extinction, JAGS, Peregrine Falcon, persistence, territory

Összefoglalás Jelen dolgozat foglalja össze a kulcsfontosságú eredményeit annak az 53 évet átfogó vizsgálat-sorozatnak, amely az egyik leghosszabb populációdinamikai kutatás a világon, és amely a francia Jura-hegységben (12 714 km^2) indult 1964-ben, a vándorsólyom *(Falco peregrinus)* állományának felmérésére. Mintegy 449 szirtet vizsgáltunk 338 lehetséges vándorsólyom territóriumon: ezek közül 287 (85%) területet legalább egyszer ivarérett madarak vettek birtokba, míg 51 (15%) esetben erre nem volt példa. A legtöbb fészkelőhelyet többször is felkeresték egy költési időszakban a foglaltság, majd később a termékenység felmérése érdekében. Ugyanakkor a felkeresett területek aránya változatos volt az évek során. Szeretnénk kiemelni a Bayes-i módszerekkel ötvözött területfoglaltsági modellek (MacKenzie *et al.* 2002, 2003) erejét a ragadozó madarak populációdinamikai adatainak elemzésében: a populáció méretének javított becslésére vonatkozóan azokra az esetekre, amikor az adott területet nem vizsgáltuk egy adott évben, valamint annak kiküszöbölésére, hogy a jobbnak tartott fészkelőhelyeket gyakrabban kerestük fel, ezért nagyobb arányban szerepeltek az adatsorban a kevésbé jó területekhez képest. Ezek a modellek lehetőséget adnak a fészkelőhelyek fennmaradásának és benépesülésének becslésére és modellezésére is, ami anélkül adhat képet a populációdinamikáról, hogy a madarakat egyedileg jelölték volna. A dinamikai viszonyok megváltozásai előre jelezhetik a populáció méretének későbbi csökkenését is.

1964 óta a megfigyelt költőpárok száma 17 (1972) és 196 (2008) között változott, ugyanakkor a felkeresett fészkelőhelyek aránya az 1964-es 43%-ról csaknem 80–90%-ra nőtt 2002 után. Ezért is lehetséges az, hogy a populáció teljes mérete alulbecsült. Erős bizonyítékot találtunk arra vonatkozóan, hogy vizsgálataink során egyes területek felkeresése előnyt élvezett másokkal szemben. Ezt figyelembe véve az 1964-es populációt 56 párra becsültünk, ami 1972-re 18 párra csökkent, majd 1995 óta gyors növekedésnek indult, és 2000–2012 között már elérte a 200–210 ivarérett párt. Ezután ismét visszaesett 170–190 párra. A meg nem látogatott költőhelyek miatt a populáció valós méretéhez képest minden egyes évben 5–39%-kal (átlagosan 11%) kevesebb adódott. A használatban lévő költőterületek aránya 78%-ról kevesebb, mint 60%-ra csökkent 1967 és 1972 között, majd gyors növekedésnek indulva a ’80-as évekre meghaladta a 90%-ot. Ez a fellendülés feltételezhetően annak köszönhető, hogy a rovarirtószerek hatásának megszűnése után az egyedek túlélőképessége is gyorsan emelkedett, és ennek következtében a költőhelyek száma ismét növekedésnek indult. Azonban a ’90-es évektől ismét csökkent a fészkelő helyek száma, ami az ivarérett egyedek túlélőképességének ismételt csökkenését jelezheti. Ezzel ellentétben a kolonizációs ráta 3%-ról 46–49%-ra emelkedett 1994 és 2001 között, majd lecsökkent a jelenlegi 33%-ra. A magasabb szirtek stabilabb költőhelynek bizonyultak a közepes vagy alacsony szirtekhez képest.

Az utóbbi 15 év csökkenő tendenciái tükrözhetik az uhu *(Bubo bubo)* növekvő elterjedése következtében fellépő fokozott ragadozó-nyomást, az emberi zavarást vagy más, eddig felderítetlen tényezőket. Fontos megjegyezni, hogy ez a csökkenő mintázat a jelen állapotok előtt is jelen volt. Ezért az itt bemutatott populációdinamikai modellek fontos előrejelzéseket adhatnak a majdani populációs változásokról. Tanulmányunk a modern analitikai módszerek előnyeinek bemutatására is szolgál, melyek javíthatják azokat a hiányosságokat, amelyek csaknem minden hasonló vizsgálatban megjelenhetnek: a költőhelyek hiányos lefedettsége és felismerése (itt csak az előbbit érintettük). A foglaltsági modellek – esetlegesen figyelembe véve a nem véletlenszerű mintavételezést – úgy tűnik, egy értelemszerű analitikai keretet adnak a ragadozó madarak populációs vizsgálatainak kivitelezéséhez.

Kulcsszavak: BUGS, dinamikus foglaltsági modell, kolonizáció, megtalálási valószínűség, kihalás, JAGS, vándorsólyom, fennmaradás, territórium

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Introduction

Long-term studies have a huge value in ecology, but they are extremely expensive to conduct and maintain. Hence, typical long-term studies in population ecology last perhaps 1–2 decades, with population studies of more than 30 years being very rare. The high costs of keeping a study alive over several decades can only be paid in a very powerful scientific study such that funding agencies will keep supporting a study over such long periods, but this is extremely rare. Most of the time, such long-term studies are "paid" by another currency: passion. It is the passion for a species, for an area, for keeping the data record unbroken, for collaborating in a group of like-minded individuals, which pushes some people to continue their population studies for the better part of a human life-time. Birds of prey (raptors and owls) have often cast an especially powerful spell on human observers, and hence, they have received perhaps a more than proportional shares of long-term population studies compared to almost any other bird groups. The Peregrine must be one of the most studied raptors in the globe, with long-term population studies being conducted in many parts of the world. Many examples of this can be gleaned in the series of books on Peregrine world conferences by Hickey (1969), Cade *et al.* (1988), Sielizki and Mizera (2009) as well as in Rau *et al.* (2015).

Here, we briefly describe what must be one of the longest-running Peregrine surveys worldwide: the population study in the French Jura mountains (Monneret 2006, 2009, 2017). The surveys started in 1964 and have been a collaborative team effort led by the first author ever since. At the time of writing this field study is in its 55th year. Here we summarize the first 53 years of this survey until 2016. We document some spatial and temporal patterns of occurrence (presence or absence of an adult pair at a site) and population size trajectories.

In particular, we highlight the power and flexibility of multi-season occupancy models (MacKenzie *et al.* 2003, 2017, Royle & Kéry 2007) as a natural analytical framework for abundance in typical raptor population studies such as ours, where a set of sites is visited over multiple breeding seasons. These models, and in particular their Bayesian implementation using Markov chain simulation (MCMC) methods, for instance in the generic statistical modeling software BUGS (Lunn *et al.* 2013), offer tremendous advantages for the analysis of abundance data in raptor population studies. Depending on the kind of data recorded, they allow one to estimate population size corrected for two kinds of observation errors which are due to (1) the lack of visits to some sites in some of the years (coverage bias) and (2) to imperfect detection, i.e. when an occupied site is visited but no pair is detected (detection bias). Unless corrected for, these errors will both lead to underestimation of population size. In this study, we show how to correct for coverage bias in raptor population studies.

In addition, the dynamic version of such multi-season occupancy models allows one to estimate and model the two processes that underlie any population change at the level of an occupied site: the site-level persistence rate and the site-level colonization rate. Persistence is the probability that a site occupied now will still be occupied in the next season, while colonization is the probability with which a site that is unoccupied now will become occupied by the next season. These two rate parameters together describe the population dynamics of a raptor population at the level of a site and can provide interesting hints at the reasons for an observed population change at the level of the population size alone. For instance, declines in persistence or colonization can be used as an early-warning signal for future population declines.

One objective of this paper is to make occupancy models more widely known among analysts of data from bird population studies, because they offer so much power to estimate population size correcting for non-visited sites (and potentially also imperfect detection) and to investigate temporal trends in the site-level dynamic rate parameters that govern the annual changes in population size. Thus, we chose a somewhat verbose or "how to" style of a manual for such analyses in the hope of making them more easily understood and more widely used.

Methods

Study area

Our study area comprised the entire French part of the wild and wonderful Jura mountains, which are a middle-elevation mountain range in France and Switzerland. The Jura is a geologically young range rich in limestone cliffs, which bends in a banana shape more than 300 km long almost from Lyon in France up to the Swiss town of Schaffhausen. At its widest, it measures about 60 km in Northwest-Southeast direction. Elevation varies from under 200 m to 1,718 m at the highest peak, the Crêt de la Neige. The highest chains are in the inner (Eastern) part, and successive chains ebb away in lesser elevations as one goes West. About half of the Jura is wooded, with the rest being mostly pasture and only little arable land, since the climate is often too cold, windy or wet for much arable agriculture. Human population density is low at 89 per km^2 on average. The French Jura is shared by the three departments Ain (5,762 km^2), Jura (4,999 km^2) and Doubs (5,234 km^2) and totals 15,995 km^2. The overall study area covered only that part of these departments that contains some cliffs or some of the rare Peregrines nesting on buildings in our study area. Applying 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 the convex hull defined by the locations of the pairs yields areas of 3,118, 4,618 and 4,978 km^2, respectively, for the Ain, Jura and Doubs, for a total 'occupied area' of 12,714 km^2.

We distinguish 'cliff objects', one or several of which form a potential Peregrine territory or a 'site'. The former are cliffs and, in a very few cases in our study area, tall buildings, that have been or could in principle be occupied by a Peregrine pair. Territories are formed by one or a cluster of cliffs and can only be occupied by a single Peregrine pair at any given time. Nesters on buildings are extremely rare in our study area, but have started to show up in very small numbers since about 2010. We have included them in our survey and this study alongside the cliff haunts. Here, we use the terms 'site' and 'territory' interchangeably. As is well-known, the definition of what represents a territory in a raptor study can be somewhat arbitrary. In particular, the territory definition by single-pair-occupancy can change over time, especially when a population is increasing or declining. During increases, double or even triple "splits" may be observed (Ratcliffe 1993), i.e. a territory formerly occupied by only one pair becomes a haunt for two or three pairs. When assigning cliff objects to territories, we naturally based our decision on the majority of years. That is, when a set of cliffs were occupied by a single pair in most years but by two pairs in just a few years, we designated these cliffs to be a single territory.

Field methods

Starting in 1964 and conducted and organized ever since by the first author, in every year members of the *Groupe Pèlerin Jura* sought to visit as many of the previously known Peregrine sites and cover as many hitherto unknown sites as possible. Either deliberately or unconsciously, most observers will first have targeted "good" sites, previously known to be occupied or to have a good history of nesting, rather than "bad" sites, known to be occupied only irregularly or to have poor breeding success.

During the first decades, field work was conducted by a small group of 5–10 dedicated people in each department, who communicated via (paper) mail and over the phone. Since the late 1990s, communication by email has become the main mode of information exchange among the members of the group. All information was centralized and housed on paper documents by the first author in the beginning and, starting in the 1990s, was migrated into an Excel data base. Each site was accurately localized on a map (IGN), to avoid misidentification of sites between observers.

Field work was conducted by individuals or small groups of observers, using binoculars and telescopes, between 1 February and early July, with most effort spent during the courtship period (15 February – 15 March) to find and confirm occupancy by single birds or pairs, in late March and early April for incubating pairs and in May to count well-grown and nearly fledged young to obtain a measure of fecundity. Most sites were visited multiple times during a breeding season, thus we expected overall detection probability to be rather high, i.e. we expected only few pairs to be overlooked at those sites that did receive visits in a given year.

Occupancy models to estimate population size and site-level colonization and persistence

The site-year format of survey data from raptor population studies

In our study, the basic survey data can be summarized in a site-by-year table of dimensions 287 (corresponding to the number of territories) by 53 (corresponding to the 53 years). A subsection of this table, with four sites and 17 years (2000–2016), and therefore a total of 68 site-year combinations, is shown as *Table 1*, and also shows the site names in the first column.

One main goal in this study is to show how to deal with one of the two types of uncertainty in such data, surrounding the interpretation of the zeroes and the missing values (= missing visits = the asterisks) in *Table 1*. For instance, perhaps we think that it is possible that an adult pair did in fact occur at Bolozon in some years after 2009 but was missed. Can we say something about the likelihood of this possibility for the 18 cases where there are zeroes in this table and if possible, factor this in to obtain an improved estimation of the population

Table 1. A small part of the data analyzed in this study, showing results of surveys of four sites in 17 years (2000–2016). A 1 and a 0 mean that a site was visited at least once in a given year and an adult pair was or was not detected. The asterisk (*) is our missing value symbol and says that no visit took place (or is recorded) for a site-year combination. In this table, out of a total of 68 site-year combinations, there is uncertainty for 44 (65%) of them: 26 are missing visits and 18 represent zero observations. For the former, obviously we have no information whether a pair was present (resulting in coverage bias), while for the latter, a pair may have been present but overlooked (resulting in detection bias)

1. táblázat Az elemzett adatok kis szelete, mely 4 terület 17 évet átölelő felmérését mutatja (2000–2016). Az 1 és 0 értékek azt mutatják, hogy adott költőhelyet legalább egyszer felkerestek az adott évben, és ott jelen volt-e ivarérett pár vagy sem. A csillag (*) a hiányzó adatokat jelöli, ami azt jelenti, hogy az adott területet nem keresték fel az adott évben, vagy nincs feljegyzés róla. Ebben a táblázatban a 68 terület-év párosításból 44 esetben (65%) figyelhető meg bizonytalanság: 26 hiányzó látogatás és 18 nulla megfigyelés. Az előbbi esetben nincs arról adat, hogy a költőpár jelen volt-e (lefedettségi eltolódás), míg az utóbbiban jelen lehetett, de nem sikerült ténylegesen megfigyelni (észlelési eltolódás)

Site	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**
Bolozon	1	*	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Chézery	*	*	1	*	0	*	*	*	0	1	*	1	0	*	0	*	*
La Fauconnière de Belleydoux	0	*	0	0	0	*	*	1	1	0	1	1	1	*	1	1	1
Fort l'Ecluse	*	1	1	1	*	0	*	*	1	*	*	*	1	*	*	*	*

size (= number of adult pairs)? And what about the 26 years in which these four sites were not visited at all? Is it not highly likely that pairs did occur at least in some of these years but had no chance of being recorded in our data simply because a site was not visited in a given year? For instance, an adult pair was recorded at Bolozon in every year between 2000 and 2008 except for 2001: would it not be natural then to assume that a pair was probably present in 2001, when no visit took place, too? But how likely is this and how would we deal with this in a formal estimate of population size? And similarly for the Fauconnière in 2001 and 2013, two years when no visit to this site was recorded. The year 2001 at that site is surrounded by years when no pair was recorded, while 2013 is surrounded by years when a pair was in fact recorded. How would this affect the likelihood that a pair was or was not present in these years with missing values and how would we deal with this in an estimate of total population size in those years? And what about the year 2009 at the Fauconnière, when the absence of an adult pair was recorded, while several years before and afterwards all had records of adult pairs? Could it not perhaps be possible that a pair was present also in 2009 but was simply missed? Can we somehow factor in this possibility when estimating population size?

And what about the processes that underlie the dynamics of the presence or absence of an adult pair at a site: can they somehow be described? And can we perhaps investigate factors that may influence Peregrine population dynamics at the level of a site occupied by an adult pair or any other descriptor of site occupancy?

It turns out that we can do all of the above by application of multi-season occupancy models to appropriate population survey data. We next describe the dynamic variant of these models in some detail, because they are so incredibly powerful for the analysis of raptor population surveys including our own, but in our opinion the power of dynamic occupancy has not yet been sufficiently recognized in the community of raptor biologists.

Dynamic (multi-season) occupancy models

Dynamic site-occupancy models (MacKenzie *et al.* 2002, 2017) are a variant of so-called multi-season occupancy models that describe change in binary systems, such as whether a set of Peregrine sites is found to be occupied or not over a series of multiple years. (Another variant are static multi-season site-occupancy models (MacKenzie *et al.* 2017), which are a simpler version that we briefly describe in the following section.). In these statistical models, the dynamics are estimated by first describing the initial state of the system, i.e. whether each site is occupied or not, as a probabilistic function of a parameter ψ (pronounced 'psi'), which is the probability that a site is occupied in the first of a series of years, which is the year 1964 in our data set. In algebra, we write this for the occupancy status $z_{i,t}$ at site *i* in year $t = 1$, e.g. presence $z_i = 1$ or absence ($z_i = 0$) of a pair at site *i* as follows:

$$z_{i,1} \sim Bernoulli(\psi_i)$$

We can read this as *'z is a draw from a Bernoulli distribution with parameter psi'*. The Bernoulli is the statisticians' equivalent for chance processes that work like the flip of a coin and produce two complementary outcomes with probability θ and $1 - \theta$, respectively. Thus, for Peregrine pair survey data, a site is either occupied or it is not, and this is governed by the occupancy probability ψ_i. This parameter is indexed by site *i*, indicating that it could be different for each site and thus could be modeled by site-specific covariates when the model is fit to a data set.

For all later years, the presence or absence of a pair in year $t = 2 \ldots T$ (where $T = 53$, corresponding to the year 2016, in our data set) is described as a recursion in terms of two random processes. These two processes describe the two transitions that are possible for a site that is initially occupied and another that is initially unoccupied. A site *i* that is occupied by a pair in year *t* can either remain occupied in the next year $t + 1$ with probability $\varphi_{i,t}$ (pronounced 'phi') or it can become abandoned in year $t + 1$ with probability $1 - \varphi_{i,t}$. Similarly, a site *i* that is unoccupied in year *t* can either be colonized in year $t + 1$ with probability $\gamma_{i,t}$ (pronounced 'gamma') or it can remain empty in year $t + 1$ with probability $1 - \gamma_{i,t}$. These two parameters are called the persistence probability φ and the colonization probability γ (Note that the former two transitions can also be described in terms of extinction probability ε, which is simply $1 - \varphi$). Both persistence and colonization parameters are here indexed by site *i* and time interval *t*. This indicates that they may differ by both site and time interval and may be modeled by covariates that vary by site or time either alone or in combination.

In algebra, we get the following for a site initially occupied by a pair (and where $z_{i,t} = 1$):

$$z_{i,t+1} \mid z_{i,t} = 1 \sim Bernoulli(\varphi_{i,t})$$

In contrast, for a site that is unoccupied at time t (and where $z_{i,t} = 0$), we get:

$$z_{i,t+1} \mid z_{i,t} = 0 \sim Bernoulli(\gamma_{i,t})$$

Thus, remarkably, by combining just three Bernoulli random processes (or, three coin-flip-like chance processes), we can describe the entire dynamics of our data on the presence or absence of a pair at each of the 287 sites for each of the 53 years in our study. We call this the description of the *true ecological process* underlying our survey data. But is this description a complete representation of our data?

Of course, any person who has ever watched Peregrines or indeed any animal or plant study species knows that a species, even when it is present in reality, is often missed when it is looked for. Hence, a datum of 0 in Table 1 (e.g. at the Fauconnière in 2009) may well refer to such an instance where a site was occupied by a pair and we did visit the site, but failed to detect the Peregrine pair. How can we make our model more realistic to account for this possibility in our data? The answer is that we simply add another Bernoulli distribution to our model. This fourth chance process describes how our "measurements", or observations, of the presence/absence of a pair at a site in a given year, $y_{i,t}$, are linked to the true state $z_{i,t}$ at that site:

$$y_{i,t} \sim Bernoulli(z_{i,t} * p_{i,t})$$

Thus, in our case, whether we detect a pair ($y_{i,t} = 1$) or not ($y_{i,t} = 0$) is the outcome of a random process and depends on two things: whether the site is occupied or unoccupied (i.e. whether we have $z_{i,t} = 1$ or $z_{i,t} = 0$) and on a second quantity, detection probability $p_{i,t}$. For an unoccupied site, we detect a pair with probability $z_{i,t} * p_{i,t} = 0 * p_{i,t} = 0$ (we assume here that we cannot erroneously detect a pair at a site that is not occupied by a pair in a given year). Otherwise, at an occupied site, we detect a pair with probability $z_{i,t} * p_{i,t} = 1 * p_{i,t} = p_{i,t}$.

Now, having added this fourth coin-flip-like random process to our statistical model for the data in *Table 1*, we have an adequate statistical model for inference about the number of pairs with which we can correct for both missing visits and imperfect detection and which moreover enables inference about the dynamic rates that underlie any change in the number of pairs. All four parameter types can be modeled, i.e. we can introduce in the model covariates or unobserved grouping factors (i.e. random-effects) to accommodate additional structure or to test whether a covariate such as elevation of a site can have an effect on occupancy or, say, whether colonization rates differ by year, department or even site. In our study, we tested for an effect of cliff height (small, medium, and big) on both persistence and colonization probability.

This is the dynamic occupancy model, which can be fitted using maximum likelihood or Bayesian techniques (Royle & Kéry 2007, MacKenzie *et al.* 2017). Bayesian model fitting is particularly appealing in our case because of the ease with which missing values are dealt with when a statistical model is fit using Markov chain Monte Carlo (MCMC) methods: missing values such as the asterisks in Table 1 are then simply estimated as a side-product of the model fitting procedure itself (Kéry & Royle 2016).

To be able to separately estimate all four types of parameters in the model, i.e. the probabilities of occupancy (ψ_i), persistence ($\varphi_{i,t}$) and colonization ($\gamma_{i,t}$) and of detection ($p_{i,t}$), we need replicate observations for at least some of the sites in at least some of the years (MacKenzie *et al.* 2003, 2017, Royle & Kéry 2007, Kéry & Schaub 2012). That is, we need individual records of the results of multiple visits to some Peregrine sites in some years (and ideally repeat visits to all sites in all years). Assuming closure, i.e. that site occupancy status z does not change within a breeding season, we can then separately estimate the parameters that describe the true ecological process (i.e. ψ_i, $\varphi_{i,t}$ and $\gamma_{i,t}$) from the parameter which describes the observation process (i.e. $p_{i,t}$).

Unfortunately, in our study (see *Table 1*), although there usually are multiple visits, we only record a summary, as if we had conducted a single visit per site and year only. Thus, in our analyses we are not able to separately estimate the parameter describing one of the two types of uncertainty described above for *Table 1*; we cannot estimate detection probability $p_{i,t}$. This means that we will underestimate occupancy and persistence probability and population size and overestimate colonization probability (Kéry & Royle, in prep.). We can assume, however, that this bias is only slight, since detection probability of Peregrine pairs can be high (Kéry & Royle 2016) and this is compounded for multiple visits. We expect combined detection probability per site and year to be greater than 90% and thus in this study will ignore the slight negative bias in population size estimates induced in our analyses by our inability to estimate detection probability.

Static (multi-season) occupancy models

A simpler variant of a multi-season occupancy model is the static model (also termed "implicit dynamics model" by MacKenzie *et al.* 2017), which can be fit to exactly the same data as a dynamic occupancy model. It lacks the parameters for the yearly dynamics and instead simply has separate occupancy and detection parameters for every year ($\psi_{i,t}$ and $p_{i,t}$). If interest focuses on population size or trends rather than dynamics, this simpler model may be preferable to the model with explicit dynamics, e.g. because the annual occupancy parameters may be constrained by a linear model with 'Year', which allows a population trend to be estimated directly. In our study, when trying to account for preferential sampling (see next section) with a more complex dynamic occupancy model, we failed to achieve numerical convergence of the algorithm and therefore had to resort to the simpler static (multi-season) occupancy model.

Preferential sampling in population studies

In many population studies such as ours, not all sites are surveyed in every year and the sites surveyed are not chosen at random. Rather, sites previously known to be occupied or to be 'good' are usually surveyed first and 'bad sites' only later, if at all. Thus, when not all sites are surveyed, the sampled sites do not form a random sample from all sites known in a study area but rather form a biased sample of higher-than-average quality. We refer to *preferential sampling* (PS) when better sites have a higher probability of being surveyed than less good sites (Conn *et al.* 2017). 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.

The solution is to fit a joint model for the survey results, with one submodel for the survey results (i.e. whether a site is found to be occupied or not, i.e. the data in *Table 1*) and another submodel for a derived variant of such a table, which simply distinguishes sites that are visited from sites that are not visited in a year. This second submodel for site visits is parameterized in terms of site visitation probability. Importantly, in such a joint model, a link between the two submodels is added, such that the *quality* of a site is used as a covariate in the submodel for visitation. In the usual case of positive preferential sampling we expect a positive effect of the site-quality-covariate on visitation probability.

We expressed site quality in two ways: first as a Gaussian random site effect on the logit transform of annual occupancy probability. This PS model variant 1 assumes that there is some average quality of a site that does not change over time and that affects the likelihood with which a site is visited. In PS model variant 2, we simply used the presence or absence of a pair at a site in year t-1 as a predictor in the model for visitation probability in year t. These PS variants of a multi-season occupancy model allow us to correct for the biasing effects of preferential sampling when extrapolating the survey results to unsurveyed sites in our attempt to estimate the true annual population size (i.e. correcting for unsurveyed sites).

Fitting the models in our study

We fit a total of five multi-season occupancy models to our full data set on 287 sites and 53 years, of which *Table 1* shows a small section. First, to estimate the trajectories of population size over the years, and to correct for sites not visited in a year, we fit four *static* multi-season occupancy models (see *Table 2* for an overview):

- Model 1 was the base model that assumed that all sites were identical in terms of their occupancy probability (i.e. no differences in site quality) and that did not account for preferential sampling (PS).
- Model 2 did not account for PS either, but assumed that each site was of different quality by adding, on the logit scale of occupancy probability, a site-specific, Gaussian random effect.
- Model 3 was an extension of model 2 that accommodates PS and where the link between occupancy probability and the visitation probability of a site was the random site effect in occupancy. We also call this PS model 1.

Table 2. Overview of four occupancy models fit to the Peregrine data to obtain estimates of population size that correct for incomplete and time-varying visitation of the 287 sites during 1964–2016

2. táblázat Négy foglaltsági modell áttekintése, melyek a vándorsólymok populáció méretének becslésére szolgálnak, figyelembe véve a 287 költőhely hiányos vagy időben változó felkeresését 1964 és 2016 között

	Site quality allowed to vary	**Site visitation random or preferential**
Model 1	No	Random
Model 2	Yes	Random
Model 3	Yes	Preferential sampling (PS variant 1)
Model 4	Yes	Preferential sampling (PS variant 2)

- Model 4 also had the random site effect in the submodel for occupancy, but used the binary indicator for presence or absence of a pair at site i during year t-1 as a predictor for visitation probability in year t. We also call this PS model 2.

Second, to infer the population dynamics, we fit a dynamic occupancy model (but without accounting for PS) with random site and random year effects and smoothed the year effects by a random walk (Link & Barker 2010) to better distinguish temporal patterns in the parameters underlying the site-level population dynamics and to gauge the variability in the quality of sites in terms of persistence and colonization probability. We also fitted an effect of cliff height (small, medium, big) on both persistence and colonization.

We fit all models with Bayesian methods in program JAGS (Plummer 2003), run from program R using package jagsUI (Kellner 2016), specifying vague priors and running the chains for sufficiently long that convergence was reached based on the Brooks-Gelman-Rubin statistic (Kéry & Royle 2016). We present posterior means as our point estimates and posterior standard deviations and 2.5 and 97.5 percentiles as Bayesian versions of a standard error and for a 95% Bayesian confidence interval (CRI).

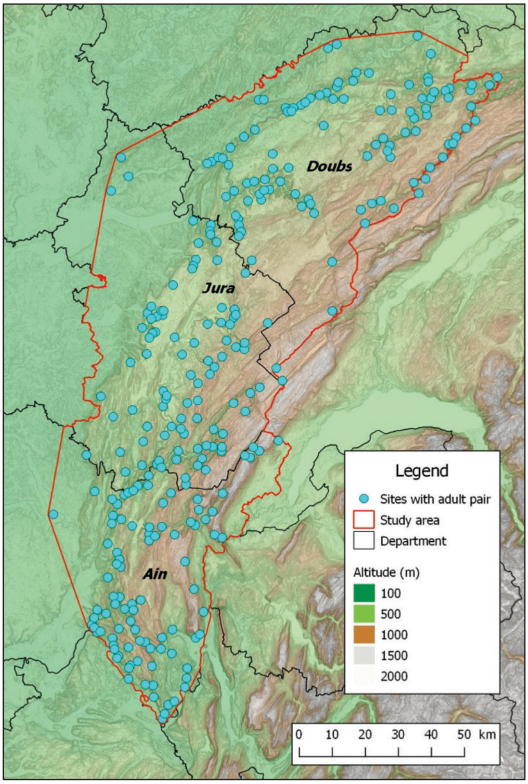

Figure 1. Distribution of 287 Peregrine sites in the French Jura mountains, stratified by three political departments (study area 12,715 km^2). A Peregrine site was defined by the observation of a Peregrine pair at least once during 1964–2016.

1. ábra A 287 vándorsólyom fészkelőhely eloszlása a francia Jura-hegységben három osztályba sorolva (vizsgálati terület mérete 12 715 km^2). Egy területet akkor tekintettünk vándorsólyom költőterületnek, ha a költőpárt legalább egyszer megfigyelték 1964 és 2016 között

Results

A brief overview of Peregrine distribution and density in the French Jura mountains

In the 53 years between 1964 and 2016, we recorded survey results from a site and a year in 11,697 cases (=site-year combinations). In 6,737 cases, a site was found to be occupied, in 6,156 cases by pairs and in 5,879 cases by adult pairs. We distinguished a total of 449 cliff sites in 338 potential Peregrine territories: 287 (85%) of these territories were found to be occupied by a pair at least once during the 53-year period, while in 51 (15%)

we never detected adult Peregrine pairs. In our analysis, we define a Peregrine site to be one such territory where a Peregrine pair was observed at least once between 1964–2016. In the Département Ain, there were 94 Peregrine territories, 91 in the Jura, and 102 in the Doubs; see *Figure 1*. The area occupied by the study population was 12,715 km^2, hence, the overall average territory density was 2.26 Peregrine sites/100 km^2. Large-scale density varied a little by department: Ain: 3.01, Jura: 1.97, Doubs 2.04. Clearly, these are maximal values, since not all territories were occupied in all years, see below.

Within a department, there was substantial local-scale variation in territory density, which we expressed by the nearest-neighbor distance (NND), i.e. the distance from one territory to the nearest neighbor. In the entire study area, NND ranged from 0.71–15.00 km, with a mean of 3.1 and a median of 2.64 km. These distances are based on the mean territory coordinates, which is often an average of multiple cliffs in a territory. The absolute minimum distance between two pairs in one year was 190 m (R. Ruffinoni unpublished, also see Kéry *et al.* 2005).

Estimation of population size using occupancy models

The observed Peregrine population (i.e. number of adult pairs) declined from 34 in 1964 to a minimum of 17 in 1972, thereafter it increased to a maximum of 191 pairs in 2012, and declined again to 169 pairs in 2016 *(Figure 2)*. However, the total of 287 sites were never all surveyed in any given year; rather, on average only about 200 sites (i.e. 70%) were visited. Hence, we would naturally assume that the observed number of pairs would underestimate the true population size. In addition, the proportion of sites visited increased from 43% per year in 1964 to over 80% during most of the 2000s *(Figure 2)*. Therefore, we would expect the degree of the underestimation of population size to vary over the years.

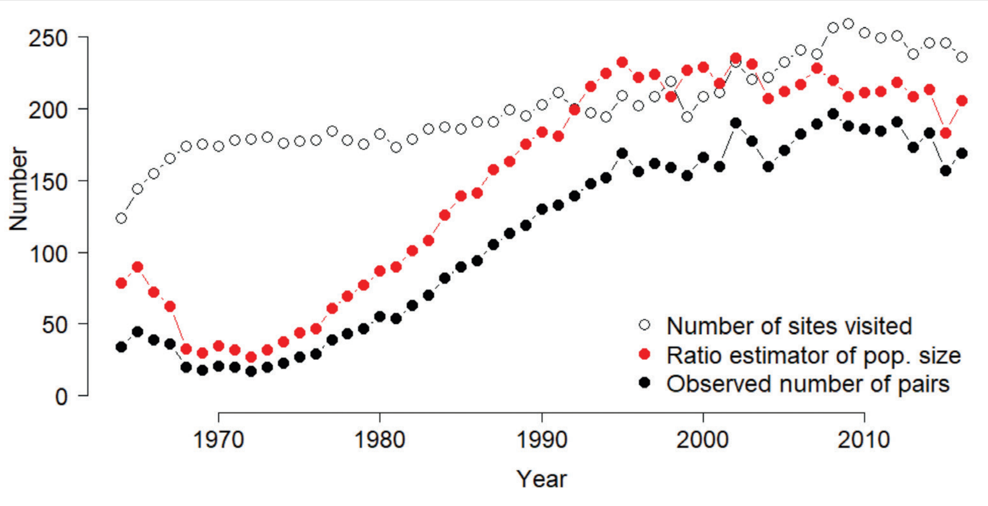

Figure 2. Number of visited sites, observed number of pairs and ratio estimator of population size for a total of 287 identified Peregrine territories in the French Jura mountains during 1964–2016

2. ábra A felkeresett költőhelyek száma, a megfigyelt költőpárok száma és a becsült populáció-méret a 287 különböző vándorsólyom territóriumon, a francia Jura-hegységben, 1964 és 2016 között

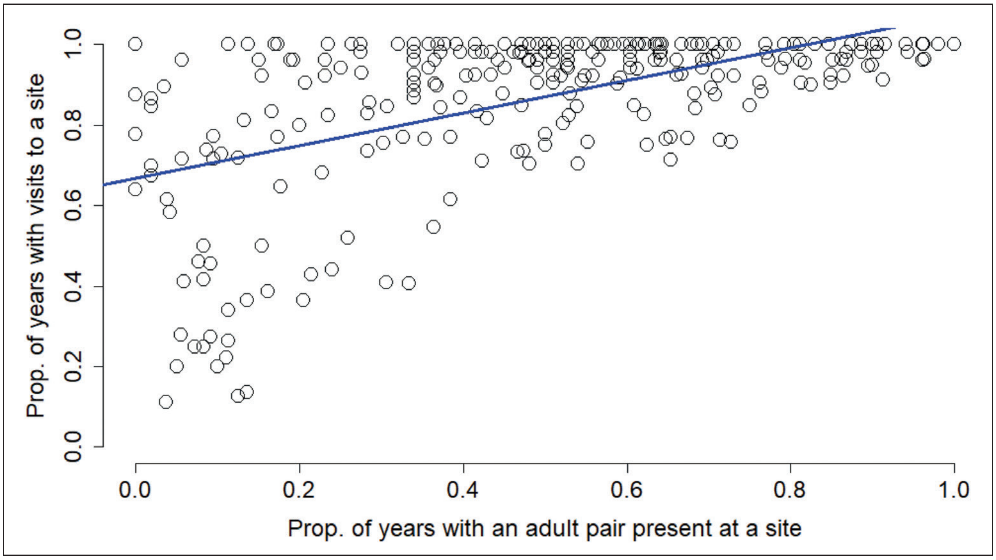

Figure 3. Relationship between the proportion of years with visits to a site (site visitation frequency) and the proportion of years in which a site was occupied (site quality). The blue line is the line of best fit of a linear regression, which explains 31% of the variance

3. ábra A meglátogatott költőhelyek években mért arányának (látogatottsági gyakoriság) és az elfoglalt helyek években mért arányának (költőhely minősége) kapcsolata. A kék egyenes egy lineáris regresszió illesztését mutatja, mely a változatosság 31%-át magyarázza

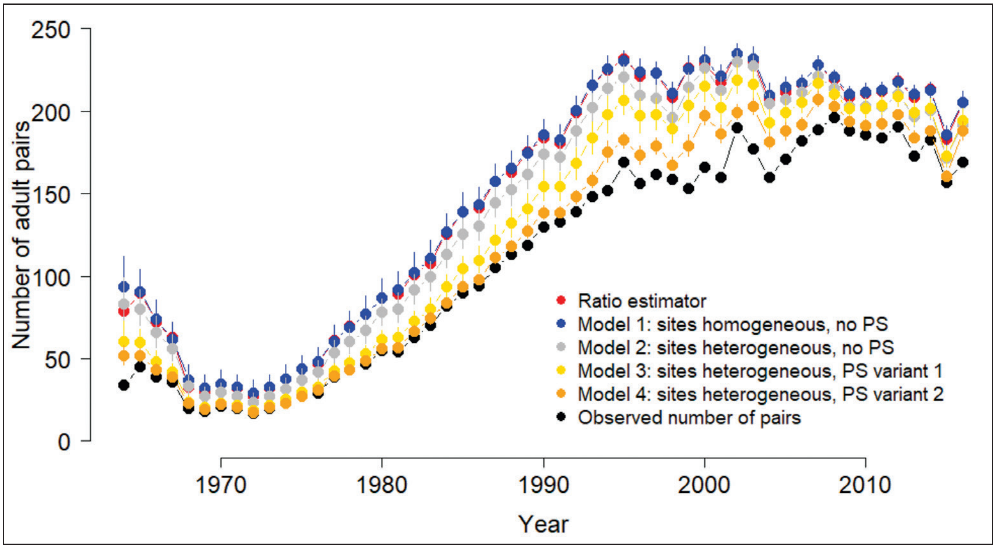

Figure 4. Observed number of pairs, ratio estimator and estimates for Peregrine population size under four occupancy models in the French Jura mountains 1964–2016, as described in the Methods and in *Table 2*.

4. ábra A költőpárok vizsgált száma, valamint a négy foglaltsági modell eredménye a francia Jura-hegység vándorsólyom populációjának becslésére 1964 és 2016 között. Bővebb leírás a Methods részben, valamint a *2. táblázat*ban található

As a first, and simplest, estimator of population size that corrects for the incomplete coverage of our surveys, we computed a ratio estimator as the observed number of pairs divided by the proportion of sites visited. This suggested that population size was severely underestimated in every year and that the magnitude of this bias varied substantially, being greatest in the initial years and during the years of the steepest recovery 1985–2005.

However, the ratio estimator is based on two assumptions that may invalidate it in practice for many raptor studies: first, it assumes that there is no difference in the quality of the sites, i.e. in the likelihood that a site is occupied, and second, it assumes that sites are visited at random. In reality, however, it is well known that there is substantial variability in the quality of raptor territories (Newton 1979, Ratcliffe 1993), such that some sites are virtually always occupied, while others only occasionally so. In addition, in many studies and especially also in ours, "good" sites are visited in preference to "bad" sites. This is illustrated in *Figure 3*, which also shows the relationship between site quality and the frequency of site visitation. Clearly, there is substantial variation in site quality, with some sites being occupied by an adult pair in every year and some only rarely if ever. Furthermore, better sites (which are more frequently occupied) were more likely to be visited than lesser sites. Thus, there was (positive) preferential sampling rather than a random visitation scheme of the sites, as required by use of the ratio estimator.

Accounting for heterogeneous site quality and preferential sampling produced substantially different population size estimates compared with the ratio estimator, which assumes the absence of both of these patterns *(Figure 4)*. The simplest occupancy model (model 1, blue symbols) essentially reproduced the estimates from the ratio estimator, because in this model, too, we make the assumptions of homogeneous site quality and random, rather than preferential, sampling. Accounting for heterogeneous site quality (model 2, grey symbols) reduced the population size estimates somewhat. Finally, accounting also for preferential sampling reduced the population size estimates even more; less so for PS variant 1 (model 3, golden symbols) than for PS variant 2 (model 4, orange symbols).

Given the strong evidence for preferential sampling in our study, we consider the population size estimates under models 3 and 4 the most reliable. However, we lacked any criterion by which to gauge which of the two was better, hence, as our best estimate at the Peregrine population size we model-averaged the estimates under these two models. In *Figure 5*, we summarize the observed number of adult pairs, the ratio estimator and the model-averaged estimates from models 3 and 4.

The model-averaged estimates (brown in *Figure 5*) indicated that the final phase of the population crash up to 1972 was steeper than observed and that the ensuing recovery was steeper, too, than what the observed number of pairs suggested. Our best correction for incomplete coverage of the 287 sites, i.e. the model-averaged estimates, indicated that population size declined from 56 pairs in 1964 to a minimum of 18 in 1972. Thereafter, the population recovered up to a maximum of 212 in 2007; since then there has been a slow decline down to an estimated 191 pairs in 2016.

The observed data underestimated the true population size by 40% in 1964 and between 10 and 20% during 1965–1969 and 1981–2007. During the "darkest years" (1970–1980) and now during the last 10 years since 2008, the underestimation was on the order of 5–10%. We

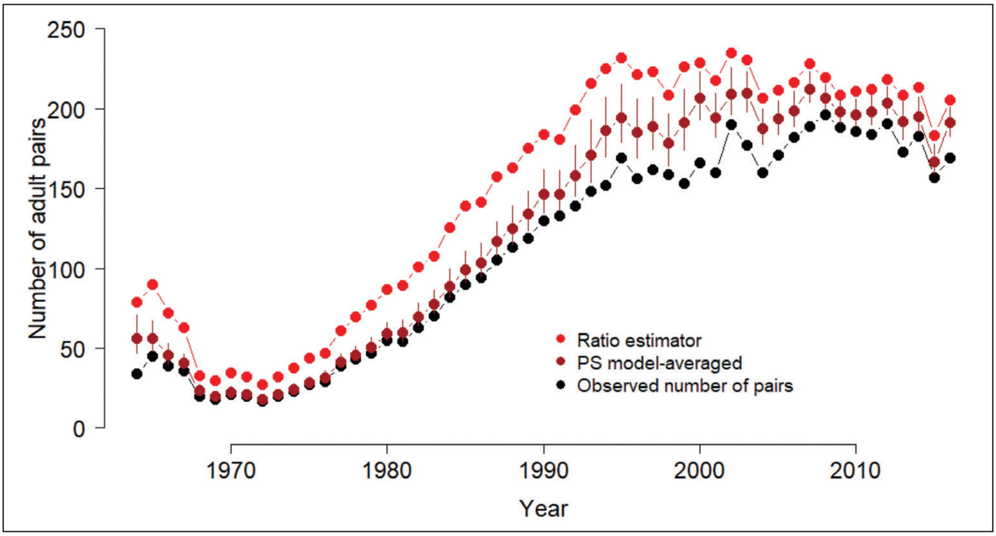

Figure 5. Observed number of pairs, ratio estimator and average between the two occupancy models with preferential sampling (models 3 and 4) for Peregrines in the French Jura mountains 1964–2016

5. ábra A költőpárok vizsgált száma, valamint azon két modell átlagolt értékei (modell 3 és modell 4), amelyekben figyelembe vettük a mintavételezés eltolódását (előnyben részesített helyek), vándorsólyom-populáció a francia Jura-hegységben 1964 és 2016 között

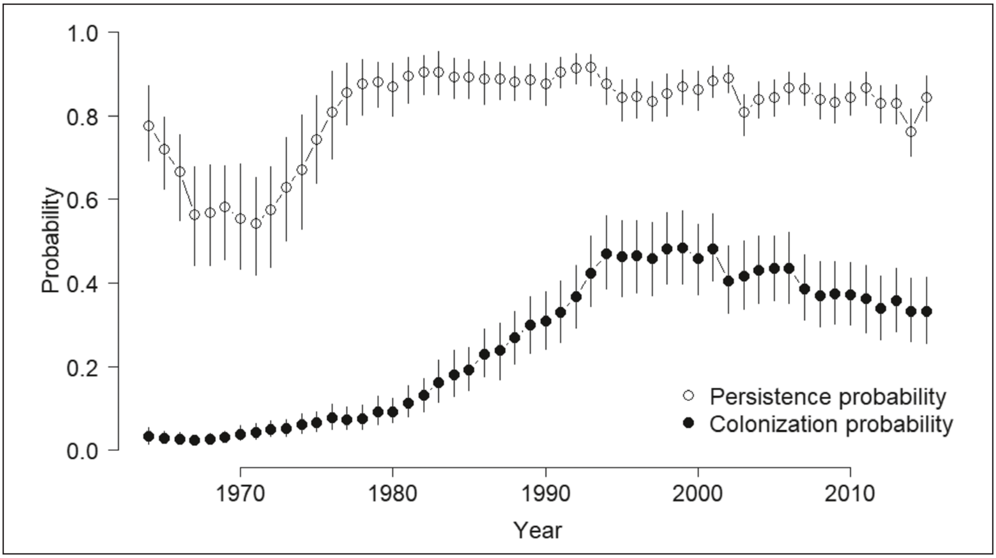

Figure 6. Estimated trajectories of the probability of site persistence (open symbols) and site colonization (solid symbols) for Peregrines in the French Jura mountains 1964–2016 based on a dynamic occupancy model

6. ábra A költőhely-foglaltság (üres körök), valamint a költőhelyek kolonizációja (sötét körök) arányainak becsült görbéi a francia Jura-hegység vándorsólyom populációjában 1964 és 2016 között, a dinamikus foglaltsági modell alapján

Table 3. Effects of cliff height (a factor with three levels: small, medium, big) on persistence and colonization probability (in %) in a dynamic occupancy model. These estimates are scaled to the beginning of the study (1964), but could equally well be estimated for any other study year. Point estimates (posterior means) and uncertainty (95% CRI) is shown for each level of the cliff height factor

3. táblázat A szirtek magasságának hatása (alacsony, közepes, magas) a foglaltsági és kolonizációs arányokra (%-ban) dinamikus foglaltsági modell alapján. Ezek a becslések a vizsgálatsorozat első évére (1964) vonatkoznak, de bármelyik másik évre alkalmazhatóak. Az átlagos értékeket és a 95%-os intervallumot minden egyes szirtmagassági kategória esetén feltüntettük

Parameter	Small cliff	Medium cliff	Big cliff
Persistence probability	73.8 (61.0–78.7)	74.0 (62.2–78.7)	81.1 (77.7– 89.2)
Colonization probability	1.5 (0.6–1.8)	2.0 (0.9–2.5)	5.1 (2.3– 6.0)

note, though, that in this analysis we could not correct for imperfect detection; hence, our population size estimates will be slight underestimates.

Inference into population dynamics using dynamic occupancy models

A second important benefit of occupancy modeling in raptor population studies is that the dynamic variants of these models provide insights into the two processes that underlie all changes in population size: namely, the probabilities of site persistence and site colonization. A dynamic occupancy model revealed annual site persistence rates that declined from 78% to less than 60% during 1967–1972, and then increased rapidly to over 90% during 1980–1990 *(Figure 6)*. This may suggest that once pesticide effects had vanished, individual survival probability increased rapidly and, as a consequence, also site persistence probability. Since the 1990s, there has been a slow but ongoing decline in persistence, which may indicate decreasing survival of adult Peregrines. In sharp contrast, colonization rates increased steadily from about 3% in the early years to maxima of almost 50% during 1994–2001 *(Figure 6)*. Since then, colonization has also declined steadily and currently reaches only about 33%. The colonization curve seems to reflect the trajectory of population size, with a greater population size producing more recruits to colonize empty territories.

Importantly, we note that both persistence and colonization rates began to decline many years before the recent population decline became apparent after about 2007: persistence started to decline more than 10 years earlier and colonization about 5 years earlier. Hence, analysis of population studies using dynamic occupancy models may provide early-warning signals for future population declines.

Big cliffs had both a greater persistence probability and colonization probability than did small or medium-sized cliffs *(Table 3)*.

Regional and site-stratified population trends

One fundamental quantity that is estimated in occupancy models is the matrix of the presence or absence of an adult pair at each site and year. We can inspect these estimates if we

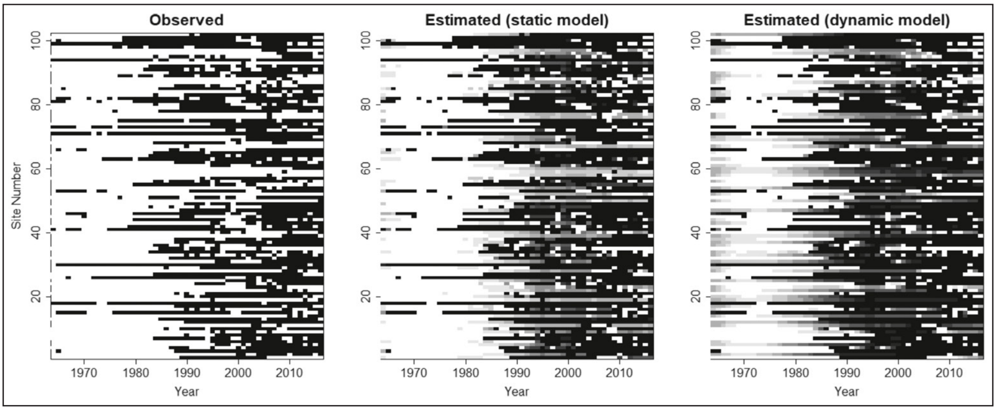

Figure 7. Illustration of the estimation of site-stratified population trends: observed presence/absence matrix of adult pairs at the 102 sites in the Département du Doubs (left) and estimates of the same matrix (corrected for missing visits) under a static (middle) and a dynamic occupancy model (right). The estimates of the presence/absence states are probabilities of presence, hence, we have shades of grey instead of only black and white. Darker shades correspond to a higher likelihood that a site is occupied

7. ábra A költőhelyek szerinti populáció méretek becslésének bemutatása: megfigyelt értékek Département du Doubs régió 102 költőhelyén (balra), ugyanannak a mátrixnak az újrabecslése (hiányzó felkeresésekre korrigálva) egy statikus (középen) és egy dinamikus modellben (jobbra). A becsült előfordulás arányban van megadva, ezért az ábra szürkeskálás, és nem csupán fekete-fehér színeket jelenít meg; a sötétebb árnyalatok egy terület foglaltságának magasabb valószínűségét jelentik

Table 4. Conditional estimates of the probability of presence of an adult pair under the dynamic occupancy model for the same sites and years as in *Table 1*. These are conditional estimates because they include the information from the observed data. Hence, whenever a pair was detected, the conditional probability of presence becomes 1

4. táblázat A dinamikus foglaltsági modell alapján kapott jelenléti arányok feltételezett becslései ivarérett költőpárok esetén, ugyanazokra a területekre és években, mint az *1. táblázatban*. A becsült értékek azért feltételesek, mert tartalmazzák a megfigyelési adatokat is. Ezért, ha egy költőpár valóban megfigyelhető volt, akkor kizárólag 1-es értéket kaphatott itt

Site	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Bolozon	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chézery	0.85	0.85	1.00	0.66	0.00	0.16	0.19	0.16	0.00	1.00	0.87	1.00	0.00	0.08	0.00	0.15	0.21
La Fauconnière de Belleydoux	0.00	0.18	0.00	0.00	0.00	0.48	0.72	1.00	1.00	0.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
Fort l'Ecluse	0.81	1.00	1.00	1.00	0.55	0.00	0.58	0.77	1.00	0.75	0.70	0.79	1.00	0.75	0.66	0.56	0.62

want to obtain the best guess as to whether any given site was or was not occupied in any given year. In our analysis, these estimates only account for missing site visits, but in more typical applications of occupancy models, the estimates would in addition correct for imperfect detection. For illustration, in *Figure 7* we compare the observed presence/absence matrix of adult pairs for the 102 sites in the Département du Doubs with the estimates of this matrix under a static and a dynamic occupancy model.

While the total population size estimates (i.e. the aggregation of these matrices across the rows) are similar for a static and a dynamic model, the site-specific estimates can be quite different. In the dynamic model, the observed data in earlier and later years influence the estimate in any given year. Thus, if there is an interest in the best possible guess of whether a site did or did not have a pair in any year when there was no visit, the dynamic model is most appropriate. For years when an adult pair was observed, this estimate will be equal to 1. For years when no visit took place, the estimate will in general be unequal to 0 or 1 and will be based on earlier or later observations of presence or absence *and* on the estimates of the probability of persistence or colonization linking that year with such observations on either side. We illustrate this in *Table 4* for the four sites that we used for illustration in *Table 1*.

As a final illustration of the use of the estimates of the site-level trends of presence or absence, we give the population size estimates for each of the three departments separately (under the average of the two occupancy models with preferential sampling; as above in *Figure 5*) and compare them to the observed number of pairs in these departments *(Figure 8)*. We see that the observation error due to incomplete coverage of the sites is different in the three departments. The observed data in the Jura are the most precise, reflecting the superior observation effort over many years in that department by the two first authors.

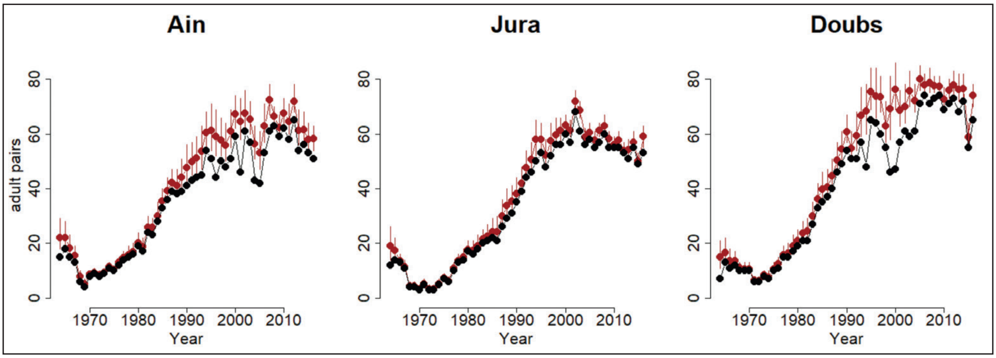

Figure 8. Regional population size estimates of Peregrine falcons for each of the three Départements in the Jura mountains 1964–2016. The brown symbols show the model-averaged estimates under the static occupancy models with preferential sampling (with 95% CRIs), while the black symbols show the observed number of pairs

8. ábra A becsült vándorsólyom populációk területenkénti bontásban a három különböző területre 1964 és 2016 között. A barna jelek a statikus foglaltsági modellek átlagértékei, ahol az eltolódott mintavételezést figyelembe vettük (95%-os intervallumokkal). A fekete jelek a ténylegesen megfigyelt párok számát mutatják

Discussion

We have briefly described what must be one of the longest-running Peregrine population studies in the entire world: that in the French Jura mountains, which was launched in 1964 and is now in its 55th year (Monneret 2006, 2009, 2017). We found the typical population size trajectory of a Peregrine population that was heavily affected by the use of pesticides: the first years of the study marked the final years of the pesticide crash. The nadir of our population was reached in 1972, with an estimated 18 adult pairs, with recovery to the maximum population size of 212 in 2007, followed by a marked decline in recent years that has taken the population size down to 191 pairs in 2016. The French Jura hosts a high density of breeding Peregrines, which was about 1.7 adult pairs per 100 km^2 at its highest, 10 years ago.

The reasons for the recent population decline are not entirely clear, but are likely to be due in the first place to predation by one of the major natural predators of the Peregrine in Europe: the Eagle Owl *(Bubo bubo)*. Itself recovering from century-long persecution, the Eagle Owl has greatly expanded its range in France in recent decades, from the original refuges mainly in the South of France where it never became extinct. A large number of Peregrine sites in the French Jura have since become occupied by Eagle Owls. Establishment of a new pair of Eagle Owls at a Peregrine site usually causes failure to produce any young, intermittent occupancy of a site by Peregrines or altogether site abandonment by the Peregrines (Monneret 2010). Thus, in one former high density patch near Baumes-les-Messieurs in the Départment du Jura, there were 7 Peregrine pairs before the arrival of the Eagle Owl, but now there are several pairs of Eagle Owls and only 3 pairs of Peregrines. Other reasons for the decline may include illegal persecution such as poisoning by pigeon fanciers or shooting by hunters, disturbance by rock climbers, delta and paragliders, bird photographers and generally people in the outdoors that may inadvertently come too close to Peregrine nesting sites.

The situation of the Peregrine in the French Jura mountains is not yet downright threatening, but the recent declines are definitely reason for concern and have changed the way in which many of us think about the Peregrine, e.g. as being entirely out of the danger zone. Rather, the recent declines have created a new awareness that all is not well and that a population that may seem very healthy in one decade may suddenly face new threats only a few years later. Hence, continuous surveillance monitoring is needed in the future, as well as efforts to curb illegal persecution, to avoid the effects of human disturbance and mitigation efforts such as creation and maintenance of artificial or improved nesting site. The first two authors have over decades expended a huge effort in Peregrine nest site creation and nest site improvement, and this has been shown to greatly boost the fecundity of a Peregrine site (Monneret *et al.* 2015). This important work should be continued over the coming decades.

A major focus of this study lies on the methodological aspects of a raptor population study such as ours, where incomplete survey coverage (not all sites can be visited in every year and the proportion visited is variable) and preferential, rather than random sampling ("good" sites are visited in preference to "bad" sites) pose severe challenges to the estimation of annual population size. We have highlighted the power of occupancy models (MacKenzie *et al.* 2002, 2003, 2017) to mitigate these problems. We have shown how the latent occupancy status of a site not visited can easily be estimated and how preferential sampling can be accommodated in a joint model for the bird population and for site visitation, where site quality is estimated in the former submodel and used as a covariate in the latter submodel (Conn *et al.* 2017). These benefits of occupancy models for the crucial objective of any population study, to assess population size, are huge and appear to make occupancy modeling a method of choice for the data analysis in many bird population studies.

But in addition, dynamic occupancy models (MacKenzie *et al.* 2003, Royle & Kéry 2007) enable one to estimate the parameters that govern the dynamics of a population, i.e. the change in population size over the years, even without individually marking the animals. These parameters are the probabilities of persistence and colonization, and we have emphasized how changes in the population size may often be preceded by earlier changes in these parameters, by many years or even decades (see also van Strien *et al.* 2011). This is what we found in our study population, where declines in persistence and colonization probabilities started in the 1990s and around 2001, respectively, although the resulting population decline only became apparent after about 2007. Hence, dynamic occupancy models can serve the important goal of providing early warning signals when something in a bird population takes a turn for the worse.

We are certainly not the first to use occupancy modeling for the analysis of raptor or owl population studies; indeed, the very first application in the paper that developed the dynamic occupancy model (MacKenzie *et al.* 2003) was for a population of cavity-nesting owls (Northern Spotted Owls *(Strix occidentalis)* (see also MacKenzie *et al.* 2009)). Some other important examples of occupancy modeling for raptor and owl population studies include Martin *et al.* (2009a, 2009b) for Golden Eagles *(Aquila chrysaetos)* and Bruggeman *et al.* (2016) for Alaskan Peregrine Falcons. The latter study provides some neat examples of how the dynamic rates governing the change in population size (i.e. persistence and colonization) can be modeled with covariates, such as cliff height, percentage of water within the territory or the distance to the nearest occupied Peregrine territory.

However, we have perhaps emphasized more than any other study before us how very powerful and suitable occupancy models are precisely for the analysis of typical population studies of raptors and owls. We believe that occupancy modeling should become a method of choice in the analysis of many population studies with unmarked individuals, where there is a clear notion of "sites", or territories that are more or less stable over the years. Of course, this is a very typical situation in raptors and owls, and hence, we believe that occupancy modeling is particularly useful for raptor and owl population studies.

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