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# Population trends of the Peregrine Falcon in Switzerland with special reference to the period 2005–2016

Marc Kéry<sup>1\*</sup>, Gabriel Banderet<sup>2</sup>, Martin Neuhaus<sup>3</sup>, Martin Weggler<sup>4</sup>, Hans Schmid<sup>1</sup>, Thomas Sattler<sup>1</sup> & David Parish<sup>5</sup>

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**Summary** We study population trends of the Peregrine Falcon (Falco peregrinus) in Switzerland with special reference to the development since 2005 and three study areas, South West Switzerland (4,993 km<sup>2</sup>, 1960–2015), the Northern Jura mountains (3,270 km<sup>2</sup>, 2005–2015) and the Canton of Zurich (1,748 km<sup>2</sup>, 2002–2015). We used dynamic occupancy models, which allow the territory-specific extinction and colonization parameters – the demographic rates (at the territory level) underlying a population trend – to be estimated. The Swiss peregrine population has developed in line with trends observed in many other countries and regions in North America and Europe: after the pesticide-induced collapse between the 1950s and 1970s, the population largely recovered up to the turn of the millennium. However, in recent years, we detected significant declines again: in SW Switzerland, the population decreased from 51 to 33 pairs during 2008–2015 (-35%), in the N Jura from 70 to 40 pairs during 2009–2015 (-43%) and in Zurich from 6-7 to 2-4 pairs during 2010-2015 (-50%). In the same time, the local extinction rate in the three study areas (more than) doubled from (0.05) 0.1 to 0.2, while the colonization rate dropped from 0.3 to 0.1 in one of the areas, while no change was detectable in the other two. We discuss two factors responsible for these strong, recent declines of Swiss peregrines: (1) predation by Eagle Owls (Bubo bubo) and (2) direct and illegal persecution by humans. In addition to these two factors, growing human disturbance (e.g. through climbers, bird photographers, paragliders, hikers, geocachers, etc.) and fatalities due to collisions with man-made structures (power lines, glass, wind turbines, etc.) are also suspected to contribute to the population decline.

Keywords: dynamic occupancy model, Jura mountains, Peregrine Falcon, persecution, predation, raptor

Összefoglalás A vándorsólyom (Falco peregrinus) populációs irányait tanulmányoztuk Svájcban – különös tekintettel annak 2005 utáni változására – három vizsgálati területen: Svájc délnyugati része (4993 km², 1960–2015), északi Jura-hegység (3270 km², 2005–2015) és Zürich kanton (1748 km², 2002–2015). Dinamikus foglaltsági modelleket alkalmaztunk, melyek egy területre jellemző kihalási és kolonizációs paraméterek – a populációs irányzatok mögött megbújó demográfiai arányok (területi szinten) – becslésére is alkalmasak. A svájci vándorsólyom populáció hasonló mintázatot mutat más országokban (Észak-Amerika és Európa) megfigyelt tendenciákkal: az 1950-es és 1970-es évek közötti fokozott rovarirtó használat után a populációk többé-kevésbé rendeződtek az ezredfordulóra. Az utóbbi időszakban azonban újabb hanyatlást figyelhetünk meg: Svájc délnyugati részén a populáció 51 párról 33 párra esett vissza 2008 és 2015 között (-35%), a Jura-hegység északi részén 2009 és 2015 között 70-ről 40 párra (-43%), és Zürich térségében 2010 és 2015 között 6–7 párról 2–4 párra (-50%). Ezzel egyidejűleg a kihalási ráta mindhárom területen közel megkétszereződött: (0,05) 0,1-ről 0,2-re, viszont a kolonizációs ráta az egyik régióban 0,3-ről visszaesett 0,1-re (a másik két régióban nem azonosítható változás). Két fő tényezőt szeretnénk kiemelni, melyek felelősek lehetnek a svájci vándorsólyom populáció ilyen mértékű csökkenéséért: (1) az uhu (*Bubo bubo*) fokozódó el-

terjedése, valamint (2) a közvetlen és törvénytelen emberi zavarások. Az említett tényezők mellett a fokozódó emberi jelenlét (hegymászók, madárfotósok, siklóernyősök, túrázók stb.), valamint mesterséges tárgyak (elektromos vezetékek, üveg, szélturbinák stb.) okozta pusztulások is hozzájárulhatnak a populáció méretének csökkenéséhez.

Kulcsszavak: dinamikus foglaltsági modell, Jura-hegység, vándorsólyom, zavarás, predáció, ragadozó madarak

- <sup>1</sup> Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland, e-mail: marc.kery@yogelwarte.ch
- <sup>2</sup> Route de la Cure 27, 1470 Lully, Switzerland
- <sup>3</sup> Juraweg 11, 3053 Münchenbuchsee, Switzerland
- <sup>4</sup> Orniplan, Wiedingstrasse 78, CH-8045 Zürich
- <sup>5</sup> Bettenstrasse 51b, 4123 Allschwil, Switzerland
- \* corresponding author

## Introduction

This study was undertaken following signs that Peregrine Falcon populations (*Falco peregrinus*) in Switzerland have recently been decreasing and in light of a growing number of reports of illegal persecution by pigeon fanciers. We focus primarily on the most recent population trends of the Peregrine in Switzerland and examine what impact the recent increase in instances of proven or suspected poisoning could have on the population.

# Methods

In order to evaluate the recent population status of the Peregrine in Switzerland, we used high-quality data from nesting territories in the three best-monitored study area in the country. Data from population surveys in Switzerland in sufficiently detailed temporal resolution are available from three areas, all situated in the North or West of Switzerland (*Figure 1*): South West Switzerland, the Northern half of the Jura mountains ("Northern Jura mountains") and the Canton of Zurich. Peregrine falcons utilize the same cliffs or ranges of cliffs for breeding purposes (Ratcliffe 1993, White *et al.* 2013), some of which have been occupied for centuries. To designate this basic "unit" for the presence of Peregrines in an area, we use the terms site, territory or eyrie interchangeably.

### Data

In South West Switzerland, Gabriel Banderet and his group of volunteers have been monitoring most of the known Peregrine sites in an area of 4,993 km<sup>2</sup> since 1960 on an annual basis, making multiple visits during the breeding season and recording occupancy and breeding success for each pair. This Peregrine survey is the longest-running population study of any avian species in Switzerland. Our analysis spans the 56 years between 1960 und 2015. For the purposes of our study, we included only the presence or absence of a breeding pair, i.e. a territorial pair which lays eggs, because the data for territorial pairs in this study was not available for the whole of the timespan.

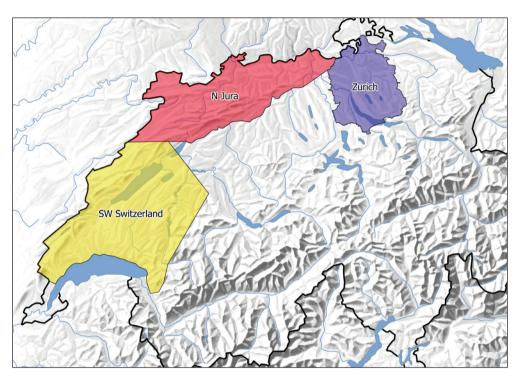


Figure 1. Map showing the three study areas for the Peregrine Falcon: South West Switzerland (yellow; Cantons of Fribourg, Neuchâtel, Vaud, Berne and Valais; monitoring group led by G. Banderet from 1960; 4,993 km²), Northern Jura mountains (red; Cantons of Berne, Jura, Solothurn, Basel-Land, Basel-Stadt, Argau; monitoring group led by M. Kéry from 2005; 3,270 km²) and the Canton of Zurich (violet; data from Orniplan AG/Martin Weggler, from 2002; 1,748 km²). Base map © Institut of Cartography ETH Zürich

1. ábra A három vándorsólyom vizsgálati terület térképe: Délnyugat-Svájc (sárga; Fribourg kanton, Neuchâtel, Vaud, Berne and Valais; a kutatócsoportot 1960 óta G. Banderet vezeti; 4993 km²), északi Jura-hegység (piros; Bern kanton, Jura, Solothurn, Basel-Land, Basel-Stadt, Argau; a kutatócsoportot 2005 óta M. Kéry vezeti; 3270 km²) és Zürich kanton (ibolya; az adatokat Orniplan AG/Martin Weggler szolgáltatták 2002 óta; 1748 km²). © Institute of Cartography ETH Zürich

In the Northern Jura mountains (the Jura mountains north of a line from La Chaux-de-Fonds to Biel/Bienne, an area of 3,270 km²) Marc Kéry, Martin Neuhaus and colleagues have been monitoring as many known territories as possible since 2005, also recording occupancy and breeding success. In our report we analysed the presence/absence of territorial pairs, i.e. independently of whether the pairs bred or not.

In the Canton of Zurich (an area of 1,748 km²), Orniplan AG (Martin Weggler, Martin Neuhaus and colleagues) have been collating all records of Peregrine Falcons at known nesting sites since 2002 and inputting them into a database from which all Peregrine breeding data were extracted on 25 April 2016. In our report we also analysed the presence/absence of territorial pairs, independently of whether the pairs bred or not.

We note therefore that we apply slightly different measures in the three study areas for assessing the population status of the Peregrine, i.e. breeding pairs in South West Switzerland

and territorial pairs in the two other study areas. As not all territorial pairs produce eggs, the number of breeding pairs will typically be lower than the number of territorial pairs. For assessing the trend – our primary objective – it is immaterial whether we analyse breeding or territorial pairs. When we refer to pairs in the following, it will be clear from the context whether we mean territorial or breeding pairs.

# Statistical analyses

The data from each of the three study areas were summarized in a matrix where the rows corresponded to the known nesting sites and the columns to the years (see *Figure 2* for an example). The elements of the matrix (the content of a cell defined by a specific site and a specific year) contain the presence (coded as a one) or the absence (coded as a zero) of a territorial pair (pairs in a territory) or of a breeding pair (pairs with proven clutches).

To analyse the population trend and the probabilities of local extinction and colonization at a site from one year to the next, we used a variant of multi-season occupancy model (MacKenzie *et al.* 2003, Kéry & Schaub 2012), also known as dynamic occupancy model (Kéry *et al.* 2013). With this variant, we omitted the customary model components which correct for false-negative observation error. Thus, no correction was made for the possibility that a site which was in fact occupied in a given year was recorded as "unoccupied" in the survey because no birds were detected although they were present. We had to make this assumption because we lacked the repeat measurements needed to correct for this type of observation error or because the "observation results" for a specific visit, although almost always noted in the field, were not recorded in the databases. We fit these models to the data from each study area, using Bayesian estimation techniques (Kéry 2010, Kéry & Schaub 2012) implemented with the program JAGS (Plummer 2003). We used so-called "vague priors" which produce estimates which, for customary sample sizes, correspond numerically to those of the also commonly used maximum likelihood estimation methods (Kéry 2010, Kéry & Royle 2016).

Although the datasets available for the three study areas contain high-quality observation data, interpreting the population trend (i.e. change in the number of pairs over the years) was complicated by gaps in the data due to the fact that in most years the sites were not entirely monitored. Thus, in order to arrive at an estimate of the total population in an area in a given year, the occupancy status for these missing years/sites had to be estimated. A great advantage of a Bayesian analysis is the ease with which such missing values can be estimated, combined with appropriate error propagation (Kéry 2010). The confidence intervals of our population estimates fully allow for the estimation uncertainty resulting from these "missing values".

In order to estimate the development over time of the colonization and extinction parameters underlying the population changes as accurately as possible and to correct for the autocorrelation over time in these parameters, we built into our models a random-walk smoothing over time (Johnson & Hoeting 2003). Using this method, it can happen that the smoothed data lie below the values actually observed because they indicate a multi-year tendency and average out annual fluctuations.

In the case of the data matrix from the South West Switzerland study area, for many years in the first half of the study period (1960 until approx. 1980) it was not always clear if a site had been surveyed and found to be unoccupied (which we denoted by a zero) or if it had not been monitored at all (which corresponds to missing data). In this dataset, we were thus unable to distinguish clearly between zeros and missing data. As we can however assume that the number of pairs observed nevertheless provides a satisfactory enough picture of the population trend of the Peregrine within this area, even in the initial years of the study period, we elected not to use a dynamic occupancy model for the site/year matrix for investigating the long-term population trend in this area but instead a simpler Poisson regression with an additive (i.e. smoothed) term over time. We conducted this analysis with the software package mgcv in program R (Wood 2006).

# Results

### South-West Switzerland

The 1960–2015 period coincides with the final phase of the worldwide pesticide-induced population crash of the Peregrine Falcon (Ratcliffe 1993), which in the year 1973 led to the complete extinction of the Peregrine in South West Switzerland. Thereafter, from the second half of the 1970s onwards the population recovered, accelerating particularly in the 1980s

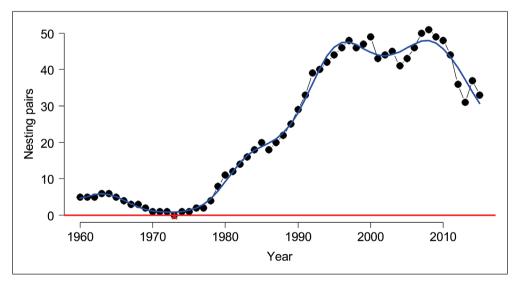


Figure 2. Population trend of the Peregrine Falcon in the South West Switzerland study area. The black dots show the number of breeding pairs detected (pairs which laid eggs). The red star highlights the year 1973 in which the Peregrine Falcon totally disappeared as a breeding species in the study area. The blue line depicts the smoothed population trend

2. ábra A vándorsólyom populációs mintázata Délnyugat-Svájcban. A fekete pontok a megfigyelt költőpárok számát jelölik (tojást is raktak). A piros csillag 1973-at jelöli, amikor a vándorsólyom nem költött a térségben. A kék vonal a populációs trend változását szemlélteti

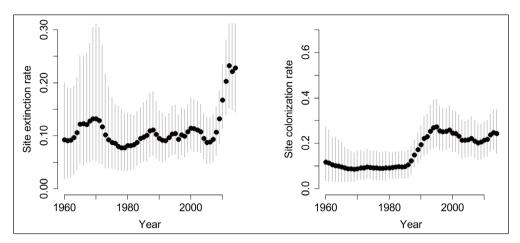


Figure 3. Time series of the demographic site extinction and site colonization rates underlying the population dynamics of the Peregrine Falcon in South West Switzerland (with 95% Bayesian credible intervals)

3. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása Délnyugat-Svájc költőhelyein (95%-os Bayesian intervallumokkal)

and 1990s and stabilizing at approximately 50 pairs since 1996. More recent years have seen a renewed decline (*Figure 2*). This figure may arguably exaggerate the original decline and subsequent recovery somewhat as the study area in the 1960s and 1970s was somewhat smaller than in subsequent years and the relatively small population in the 1960s is also influenced as a result.

Since 2000 it can be seen that the Peregrine suffered a population decline from 51 (2008) to only 33 pairs (2015). Thus, during this seven-year period the number of breeding pairs in South West Switzerland decreased by 35%.

More detailed analysis of the population dynamics by estimating the demographic rates (probability of site extinction or local colonization) in the dynamic occupancy model showed that the extinction rate shot up towards the end of the study period (from approx. 2008) to reach values well in excess of those at the end of the pesticide crash in the 1960s (*Figure 3* left). By contrast, the colonization rate in South West Switzerland increased after the pesticide crash and, in the last ten years, remained roughly in line with the values of the preceding years (*Figure 3* right).

### Northern Jura mountains 2005–2015

The Peregrine population in the North Jura study area declined from approx.70 pairs (in the years 2005–2009) to only around 40 pairs in the final year of the study period (2015) (*Figure 4*). This represents a decrease of 43% in the space of only 6 years (2009–2015).

Analysis of the demographic rates in the North Jura study area shows that, over the same time span, the likelihood of extinction at an occupied site doubled from 10 to 20% (*Figure 5* left) while the likelihood of colonization of an unoccupied site dropped from approx. 30% to not much more than 10%.

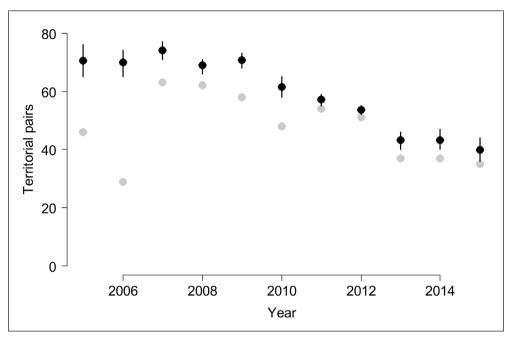


Figure 4. Population trend of the Peregrine Falcon in the Northern Jura mountain study area during the 2005–2015 period. The grey dots correspond to the number of pairs observed, which is however distorted due to annual fluctuations in the number of sites monitored. The black dots depict the corrected number of territorial pairs, accounting for the likely occupancy status of sites not visited in a given year (with 95% Bayesian credible intervals)

4. ábra A vándorsólyom populációs mintázata az északi Jura-hegységben 2005 és 2015 között. A szürke pontok a megfigyelt költőpárok számát jelölik, azonban a felkeresett költőhelyek éves változásával torzítottak. A fekete pontok az adott évben kihagyott költőhelyek lehetséges foglaltságával javított értékeket szemléltetik (95%-os Bayesian intervallumokkal)

### Canton of Zurich 2002-2015

Occupancy, i.e. the presence or absence of a territorial pair, for the eight Peregrine sites known since 2000 is shown in detail in *Table 1*. Using the Bayesian implementation of the dynamic occupancy model allowed us to correct for annual fluctuations in the number of nesting sites monitored (*Figure 6*) and suggested that the population numbered six to seven pairs up until 2010, thereafter declining successively to only 2–4 pairs (2014/2015). This represents a drop of at least 50% within the space of only 4–5 years.

Analysis of the demographic rates shows that in the same period the likelihood of extinction of an occupied site has multiplied from approx. 5 to over 20% (*Figure 7* left). The likelihood of colonization of an unoccupied site can only be estimated imprecisely owing to the very small numbers involved but here too the estimates point to a decline at the end of the study period (*Figure 7* right).

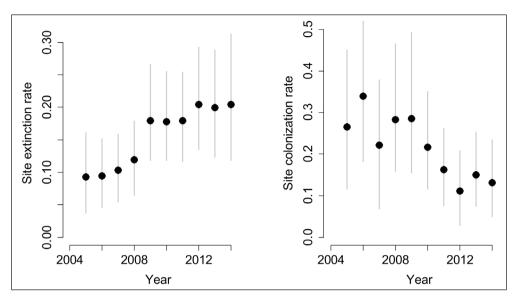


Figure 5. Time series of the demographic rates (extinction and colonization rates) underlying the population dynamics of the Peregrine Falcon in the Northern Jura mountains study area (with 95% Bayesian credible intervals in grey)

5. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása az északi Jura-hegység költőhelyein (95%-os Bayesian intervallumokkal)

Table 1. Occupancy of the eight Peregrine Falcon sites known in the Canton of Zurich since 2000 according to data provided by Orniplan AG (M. Weggler) and M. Neuhaus. A 1 signifies that a Peregrine pair was detected at a site in a given year and a 0 that the site was monitored but no Peregrine pair was detected. 'NA' signifies a missing value, i.e. that a site was not monitored in a given year

1. táblázat Az ismert vándorsólyom költőhelyek foglaltságai Zürich kantonban 2000 óta Orniplan AG (M. Weggler) és M. Neuhaus által szolgáltatott adatok alapján. 1 jelöli, ha az adott területen ténylegesen megfigyeltek költő vándorsólyom párt az adott évben, és 0 mutatja, ha a területet felkeresték, de nem sikerült költőpárt megfigyelni. NA a hiányzó adatokat jelenti, vagyis azokat az eseteket, amikor a területet egyáltalán nem monitorozták egy adott évben

Site	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Α	1	1	NA	1	1	1	1	1	1	1	1	1	1	1
В	NA	NA	NA	NA	1	1	1	1	1	NA	1	0	0	0
С	1	1	1	1	1	1	1	NA	1	0	0	0	0	0
D	NA	0	0	0	0	0	1							
Ε	1	1	1	1	1	1	NA	NA	1	1	1	1	1	NA
F	NA	1	1	1	1	1	1	1	1	0	1	0	0	1
G	1	NA	NA	NA	1	1	1	1	1	1	0	1	0	0
Н	1	1	1	1	1	1	NA	1	1	1	0	0	0	0

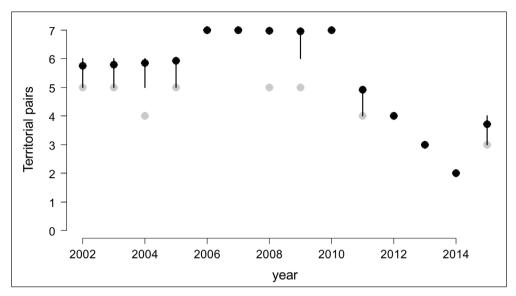


Figure 6. Population trend of the Peregrine Falcon in the Canton of Zurich during the 2002–2015 period. The grey dots correspond to the number of pairs observed which is however distorted due to annual fluctuations in the number of sites monitored. The black dots depict the corrected number of territorial pairs (with 95% Bayesian credible intervals)

6. ábra A vándorsólyom populációs mintázata Zürich kantonban 2002 és 2015 között. A szürke pontok a megfigyelt költőpárok számát jelölik, azonban a felkeresett költőhelyek éves változásával torzítottak. A fekete pontok az adott évben kihagyott költőhelyek lehetséges foglaltságával javított értékeket szemléltetik (95%-os Bayesian intervallumokkal)

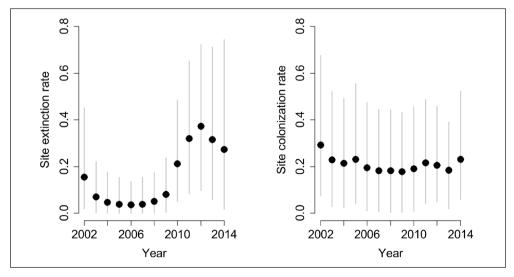


Figure 7. Time series of the demographic rates (site extinction and colonization rates) underlying the population dynamics of the Peregrine Falcon in the Canton of Zurich (with 95% Bayesian credible intervals in grey)

7. ábra A vándorsólyom populációdinamikája mögött rejlő kihalási és kolonizációs ráták időbeli megoszlása Zürich kanton költőhelyein (95%-os Bayesian intervallumokkal)

# Discussion

# Population trends and their demographic drivers

The population trend of the Peregrine Falcon in Switzerland largely mirrored that observed in many other countries in Europe and North America (Ratcliffe 1993, White *et al.* 2013): following a population crash caused by environmental toxins like the pesticides DDT and Dieldrin between the 1950s and the 1970s, numbers largely recovered again up until 2000. The Peregrine thus embodies one of the great success stories in nature conservation, in Switzerland and globally.

In more recent years, however, the trend has no longer been so positive, a fact that is still little known and hardly published. Our investigation shows that in three of the best monitored sub-populations of the Peregrine Falcon in Switzerland (South West Switzerland, Northern Jura mountains, Canton of Zurich), numbers in the past 10 years dropped by between 35 and at least 50%: in the South West Switzerland study area from 2008–2014 from 51 to 33 breeding pairs (-35%), in the Northern Jura mountains study area from 2009–2015 from 70 to 40 territorial pairs (-43%) and in the Canton of Zurich from 2010–2014/2015 from 6–7 to only 2–4 territorial pairs (corresponding to a decline of 50% or more). These unexpectedly sharp declines in all three populations are astonishing, and their synchronicity (they all began to show between 2008 and 2010) appears to point to common causes operating on a wide geographic scale.

The demographic drivers behind this population trend were investigated by analysing the local, or site, extinction rates (i.e. the likelihood of an occupied nesting site being abandoned the following year) and the local, or site, colonization rates (i.e. the likelihood of an abandoned site being reoccupied the following year) within the framework of a dynamic occupancy model (MacKenzie *et al.* 2003). The analysis showed that over the same period (beginning around 2008–2010) the extinction rate rose sharply in all three study areas (South West Switzerland and North Jura from 0.1 to 0.2, Canton of Zurich from around 0.05 to 0.2) while the colonization rate in one study area (North Jura) dropped sharply (from 0.3 to 0.1) but in the other two study areas, South West Switzerland and the Canton of Zurich, showed no clear change throughout the period of the recent population declines.

Additionally, in the past 5 years, more and more immature (one-year-old) Peregrines have been found paired in the territories (G. Banderet, M. Kéry, M. Neuhaus pers. obs.). In a long-lived species like the Peregrine this suggests that the "reserve" of adult "floaters", i.e. birds not yet holding a territory but able to take over if a territorial bird is lost, is exhausted. One-year-old Peregrines breed far more rarely and less successfully than adults so that a significant proportion of paired one-year-olds will automatically mean a drop in reproduction within a Peregrine population.

# What factors influence the demographic rates underlying the population trends?

Based on the data and information available within Switzerland and from neighbouring countries (France and Germany), two factors in particular would appear to be to blame for the

recent declines in Swiss Peregrine numbers: the recovery in the Eagle Owl (*Bubo bubo*) population and renewed human persecution, probably predominantly through poisoning by pigeon-fanciers. Two further factors, i.e. human disturbance (climbers, bird photographers, paragliders, hikers, geocaching etc.) and additional mortality due to collisions with man-made infrastructure (power lines, fences, windows, wind turbines, vehicles) probably also played a role, especially since the incidence of both sets of causes has greatly increased in recent years.

The Eagle Owl is the primary predator of the Peregrine falcon and to a large extent shares the same breeding habitat: mainly high cliffs. Up until the 1980s, the Eagle Owl in Switzerland had been largely exterminated for many decades outside of the Alps. Subsequently, isolated pairs began to establish themselves following local reintroduction efforts, especially within the Canton of Basel-Land within the Northern Jura mountains study area. The past 10–20 years, however, have seen a widespread and almost explosive recolonization of much of Switzerland probably fuelled primarily by immigration from naturally expanding populations both in Germany and France (Rau *et al.* 2015). As a result, numerous pairs of Eagle Owls have established themselves in cliffs previously occupied by Peregrine falcons within all three study areas. As a rule, this means these sites are abandoned by the falcons (or that would-be breeders run a serious risk of being predated by the neighbouring Eagle Owls). The population recovery of the Eagle Owl in Switzerland is in full swing. In the North Jura study area, for example, Eagle Owl density is probably now comparable to that of the Peregrine (unpublished data from the Northern Jura mountains monitoring group).

A second important factor to be envisaged as partly responsible for the declining Peregrine population is direct persecution, primarily through poisoning by pigeon-fanciers. There are indications of such illegal practices mainly in the Zurich and Basel areas but locally also from East Switzerland and Aargau. Although only an indicator and not hard and fast proof, the synchronicity between the incidence of suspicious Peregrine deaths (instances of poisoning) and the population decline from 2008–2010 is nonetheless striking.

# Can the poisoning of just a few Peregrines significantly impact population levels?

For the small to medium-sized Peregrine populations in the three study areas the answer is definitely affirmative. Peregrines are relatively long-lived raptors with a comparatively low rate of reproduction. In animals with a similar life history, the survival rate for reproducing adults is especially critical for maintaining population levels (Saether & Bakke 2000). For instance, Schaub *et al.* (2009) have shown that in a small but growing population of Bearded Vultures in the Alps numbering 50 adult individuals, 2–3 additional deaths (e.g. as a result of persecution) would in all likelihood lead to the population's long-term extinction.

We owe a particularly relevant and highly topical study to Altwegg *et al.* (2014), who examined an urban population of Peregrine falcons breeding on buildings in Cape Town, South Africa from 1997–2010. During the study period this population expanded sharply from 3 to 18 breeding pairs. Altwegg and his colleagues were, however, able to show that this urban population was strongly dependent on immigration from the surrounding countryside (e.g. from the cliffs of Table Mountain) and that without this immigration the urban population would not have increased so strongly but instead would have declined or at best

stagnated. In their "integrated population model" (IPM) they were even able to calculate how many adult Peregrines immigrated into the urban environment annually and began to breed there; it was no more than 1 or 2 birds per year.

This study by Altwegg *et al.* (2014) shows emphatically that in small populations each individual bird matters. To obtain comparable figures for the three Swiss populations, we can simply extrapolate proportional to the population size. If in a population of 18 pairs (at the end of the study period of Altwegg *et al.* 2014), a maximum of two individuals can make the difference between an increasing and a decreasing population, this would similarly hold true for the Peregrine in Switzerland. In a population like the size of South West Switzerland's, which at 50 pairs is 2.78 times bigger than Cape Town's (18 pairs),  $2.78 * 2 \approx 6$  Peregrine fatalities could therefore make the difference between a stable and declining population. By analogy, in the Northern Jura mountains with its original count of approx. 70 pairs, the loss of  $(70/18) * 2 \approx 8$  individuals per year would then lead to a steep decline instead of a stable population (as could still be observed in 2005). And transposing Altwegg *et al.* (2014)'s findings to the very small Zurich sub-population strongly suggests that even a single poisoned Peregrine per year could lead to a critical decline in the population level.

Of course, these extrapolations presuppose that productivity in the populations of Cape Town and Switzerland is comparable. However, the population studied by Altwegg *et al.* (2014) had a higher productivity in this urban population breeding largely in nestboxes than in "natural populations" like those in Switzerland, where eyries are frequently more exposed to the elements and natural terrestrial predators like martens and foxes. Where productivity is lower, however, immigration becomes even more important. Thus, it can be assumed that the above extrapolations we made for Switzerland are more on the conservative side, and that the loss of even fewer individuals than those cited above could already have a critical impact on the population level.

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### References

- Altwegg, R., Jenkins, A. & Abadie, F. 2014. Nestboxes and immigration drive the growth of an urban Peregrine Falcon *Falco peregrinus* population. Ibis 156: 107–115. DOI: 10.1111/ibi.12125
- Johnson, D. S. & Hoeting, J. A. 2003. Autoregressive models for capture-recapture data: A Bayesian approach. Biometrics 59: 341–350. DOI: 10.1111/1541-0420.00041
- Kéry, M. 2010. Introduction to WinBUGS for Ecologists. A Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, Burlington, MA.
- Kéry, M., Guillera-Arroita, G. & Lahoz-Monfort, J. J. 2013. Analysing and mapping species range dynamics using dynamic occupancy models. Journal of Biogeography 40: 1463–1474. DOI: 10.1111/jbi.12087
- Kéry, M. & Royle, J. A. 2016. Applied hierarchical modeling in ecology Modeling distribution, abundance and species richness using R and BUGS. Vol. 1. Prelude and Static Models. Elsevier/Academic Press
- Kéry, M. & Schaub, M. 2012. Bayesian population analysis using WinBUGS A hierarchical perspective. Academic Press, Waltham, MA.
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. & Franklin, A. B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84: 2200–2207. DOI: 10.1890/02-3090
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik, K., Leisch, F. & Zeileis, A. (eds.) Proceedings of the 3<sup>rd</sup> International Workshop in Distributed Statistical Computing (DSC 2003), March 20–22, Technische Universität, Vienna, Austria, pp. 1–10.
- Ratcliffe, D. A. 1993. The Peregrine Falcon. Poyser, Calton
- Rau, F., Lühl, R. & Becht, J. 2015. 50 Jahre Schutz von Fels und Falken. Ornithologische Jahreshefte für Baden-Württemberg, Band 31. (Sonderband, November 2015) (in German)
- Saether, B-E. & Bakke, O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653. DOI: 10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2
- Schaub, M., Zink, R., Beissmann, H., Sarrazin, F. & Arlettaz, R. 2009. When to end releases in reintroduction programmes: demographic rates and population viability analysis of Bearded Vultures in the Alps. Journal of Applied Ecology 46: 92–100. DOI: 10.1111/j.1365-2664.2008.01585.x
- White, C. M., Cade, T. J. & Enderson, J. H. 2013. Peregrine Falcons of the World. Lynx Editions, Barcelona, Spain
- Wood, S. N. 2006. Generalized additive models. An introduction with R. Chapman & Hall/CRC, Boca Raton, USA

