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Tawny Owl *Strix aluco* as an indicator of Barn Owl *Tyto alba* breeding biology and the effect of winter severity on Barn Owl reproduction

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In the temperate zone, food availability and winter weather place serious constraints on European Barn Owl *Tyto alba* populations. Using data collected over 22 years in a Swiss population, we analysed the influence of early pre-breeding food conditions and winter severity on between-year variations in population size and reproductive performance. To estimate pre-breeding food conditions, we attempted a novel approach based on an index that combines Tawny Owl *Strix aluco* reproductive parameters and the occurrence of wood mice *Apodemus* sp. in their diet. Tawny Owls breed earlier in the season than Barn Owls and are strongly dependent on the abundance of wood mice for breeding. This index was strongly positively associated with the number of breeding pairs and early breeding in the Barn Owl. Winter severity, measured by snow cover and low temperatures, had a pronounced negative influence on the size of the breeding population and clutch size. Food conditions early in the breeding season and winter severity differentially affect the Barn Owl life cycle. We were able to use aspects of the ecology and demography of the Tawny Owl as an indicator of the quality of the environment for a related species of similar ecology, in this case the Barn Owl.

Keywords: *Apodemus*, food condition, reproduction, winter, wood mice.

A major goal for ecologists is to monitor population trends and make predictions about them. This is not an easy exercise because it not only requires a precise knowledge of ecological factors that are responsible for population size fluctuations but also the ability to measure these factors reliably. Given the complexity of ecosystems and the need to distinguish changes due to anthropogenic activities from those caused by natural processes (Magurran *et al.* 2010), we need to derive integrative measures of the factors that influence the population dynamics of the species of interest. The difficulties in monitoring some ecological factors known to drive population size variation may require consideration of surrogate measures. This approach may be particularly fruitful in ornithology when, for instance, the aim is to identify the determinant role of food supply on reproductive parameters. In many species, such as passerines and raptors, measuring the availability of caterpillars or rodents is time-consuming and technically difficult when applied at a large scale and over many years.

To address these problems, we tested the ecological correlates of reproductive success and population dynamics of one bird species using as a proxy the reproductive parameters of a second species that is highly sensitive to certain ecological factors. Specifically, our aim was to investigate the role played by food supply early in the season on the breeding performance of Western Barn Owls *Tyto alba*. This species shows pronounced inter-annual variation in population size (Taylor 1994) but the extent to which pre-breeding food conditions account for these inter-annual variations is unclear,

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whereas winter conditions are known to play a very important role (Altwegg *et al.* 2006). Measuring food supply requires the monitoring of vole populations over many years, as has been achieved in Scandinavia to study the role of food on population dynamics of owls (Lehikoinen *et al.* 2011), but logistical and funding constraints can prevent such work. Here we propose an alternative approach based on the observation that population size and reproductive parameters of Tawny Owls *Strix aluco* are strongly related to the availability of wood mice *Apodemus sylvaticus* and *Apodemus flavicollis* (Roulin *et al.* 2009) (Table 1). Because Tawny Owls breed early in the season, on average 7 weeks before the Barn Owl, and their reproductive potential is strongly dependent on the availability of wood mice (Roulin *et al.* 2009, Table 1), their reproductive success and population size can be considered appropriate surrogates of the abundance of wood mice just before the start of the Barn Owl breeding season. Barn Owls also consume wood mice early in their own breeding season (A. Roulin, unpubl. data), and hence the correlation between Tawny Owl and Barn Owl reproductive parameters would give information about the potential role played by wood mice early in the breeding season (i.e. spring) in Barn Owl breeding biology. Such an approach can allow biologists working on different species to share data to test the interdependence of certain ecological factors.

Compared with other owls and raptors, the Barn Owl is extremely sensitive to harsh winters (Schönfeld *et al.* 1977, Chanson *et al.* 1988, Muller 1989, Handrich *et al.* 1993, Marti 1994, Altwegg *et al.* 2003, 2006). This gives us the opportunity to evaluate the relative impact of winter weather and pre-breeding food conditions as assessed by Tawny Owl reproductive parameters obtained in the same region. To this end, we used 22 years of data collected in western Switzerland.

Table 1. Relationship between the proportion of prey remains that were wood mice *Apodemus* spp. in Tawny Owl nests and the Tawny Owl annual breeding parameters. Sample size is 22 years.

Tawny Owl breeding parameter	Pearson's correlation coefficient (*r*)	*P*
Annual number of breeding pairs	0.62	0.0022
Annual mean laying date	−0.81	< 0.0001
Annual mean clutch size	0.73	< 0.0001
Annual mean % hatching success	0.25	0.27
Annual mean number of fledglings	0.85	< 0.0001
Annual mean % of failed nesting attempts	−0.81	< 0.0001

METHODS

Study site

Data were collected between 1990 and 2011 around the city of Payerne (46°49′N, 6°57′E). The area consists primarily of agricultural land and covers 480 km^2 at an elevation of 430–710 m. We monitored 109 Tawny Owl nestboxes, and captured 902 different adult Barn Owls (534 females and 368 males) and 3531 young fledged from 176 boxes (see Frey *et al.* 2011 for a scaled map of the study area). All data refer to breeding attempts in nestboxes, whose number did not vary between 1990 and 2011.

Tawny Owl and Barn Owl breeding parameters

For both species we recorded laying date, clutch size, hatching success (i.e. proportion of eggs that hatched) and number of fledglings for each nesting attempt. The laying date is the date on which the first egg of each clutch was laid, determined from the age of the first-hatched nestling at the first nest visit and assuming a period of 32 days for incubation (Galeotti 2001, Roulin 2004a). Brood size was checked until the youngest nestling was approximately 55 days of age to know how many nestlings died and how many nestlings fledged. Barn Owls (but not Tawny Owls) can produce up to two broods annually but because these second breeding attempts occur much later in the season, they could be influenced by factors other than winter harshness and early pre-breeding food conditions. For this reason, we excluded them from data analyses.

Winter severity

Data were obtained from the Swiss Meteorological Institute for Payerne, which is situated in the centre of the study area. Daily weather data were extracted for daily mean temperature (°C) and snow depth (cm) at 17:40 h. The seasonal temperature and precipitation averages and ranges during the study period are described in Table 2.

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Table 2. Seasonal climate (average daily temperature and precipitation) in the study area between 1990 and 2011.

	Temperature (°C)		Precipitation (mm)	
	Mean (± se)	Range: seasonal means	Mean (± se)	Range: seasonal means
Winter (Dec–Feb)	1.3 ± 0.09	−0.62 and 3.25	1.7 ± 0.08	0.89 and 3.60
Spring (Mar–May)	9.53 ± 0.11	8.17 and 11.09	2.2 ± 0.04	1.03 and 4.46
Summer (Jun–Aug)	18.18 ± 0.07	17.01 and 21.75	2.9 ± 0.02	1.86 and 5.47
Autumn (Sep–Nov)	9.55 ± 0.12	5.31 and 9.35	2.54 ± 0.13	1.12 and 3.97

To obtain an index of winter severity we performed a principal components analysis (Table 3) based on a correlation matrix including average winter temperature and number of days with more than 5 cm of snow on the ground between 1 December and the last day of February. The first principal component with an eigenvalue above 1 was positively correlated with snow days and inversely correlated with temperature and was considered a direct measure of severity in our analyses. The mean total number of days with more than 5 cm of snow was 4.8 ± 1.6 days per year (range: 0–31 days) (Fig. 1). The two variables describing winter severity (temperature and snow days) were significantly correlated (Pearson's $r = -0.51$, $n = 22$ years, $P = 0.016$).

Table 3. Loadings of principal components analyses to describe (A) winter harshness and (B) pre-breeding food conditions. Principal component 2 is shown for descriptive purposes only.

	Principal component 1	Principal component 2
(A) Winter harshness		
Average winter temperature	−0.71	0.71
Winter days with snow cover > 5 cm	0.71	0.71
Eigenvalue	1.51	0.49
Cumulative variance	0.75	1.0
(B) Pre-breeding food conditions		
Number of Tawny Owl breeding pairs	0.40	0.79
Mean Tawny Owl laying date	−0.45	0.43
Mean Tawny Owl clutch size	0.45	0.25
Mean Tawny Owl brood size at fledging	0.48	−0.22
Proportion *Apodemus* sp. in Tawny Owl prey remains	0.45	−0.28
Eigenvalue	4.0	0.51
Cumulative variance	0.80	0.90

Pre-breeding food conditions

Pre-breeding food conditions for Barn Owls were described by an index combining the percentage of prey remains found in Tawny Owl nestboxes that were wood mice and Tawny Owl breeding parameters (number of breeding pairs, laying date, clutch size and brood size at fledging) recorded in the same years and region. Prey remains were found during visits to Tawny Owl nests.

In our study population, the percentage of prey items consumed by Tawny Owls that are wood mice averaged 65% (Roulin *et al.* 2008). Moreover, the mean annual number of wood mice per Tawny Owl nest was strongly correlated with the annual percentage of prey remains that were wood mice in Tawny owl nests ($r = 0.83$, $n = 22$ years, $P < 0.0001$), and the annual percentage of prey remains that were wood mice in Tawny Owl nests was strongly correlated with the mean number of wood mice per nestling Tawny Owl and with the mean number of prey remains (wood mice and others) per nestling ($r = 0.81$, $n = 22$ years, $P < 0.0001$ and $r = 0.59$, $n = 22$ years, $P = 0.0083$, respectively). This confirms that the proportion of prey remains that are wood mice is a good proxy of the quantity of prey available to breeding Tawny Owls. Although the two owl species occupy different habitats, wood mice also make up 18% of items captured annually in Barn Owl diet, and 52% in spring when Common Voles *Microtus arvalis* are less abundant (Roulin 2004b). Furthermore, the annual percentages of wood mice remains in Tawny Owl and Barn Owl nests are highly correlated (Pearson's $r = 0.67$, $n = 21$ years, $P = 0.0009$), further suggesting that Tawny Owl diet and breeding success can be used as a surrogate for wood mouse abundance.

We created the index of pre-breeding food conditions by extracting the first component of a

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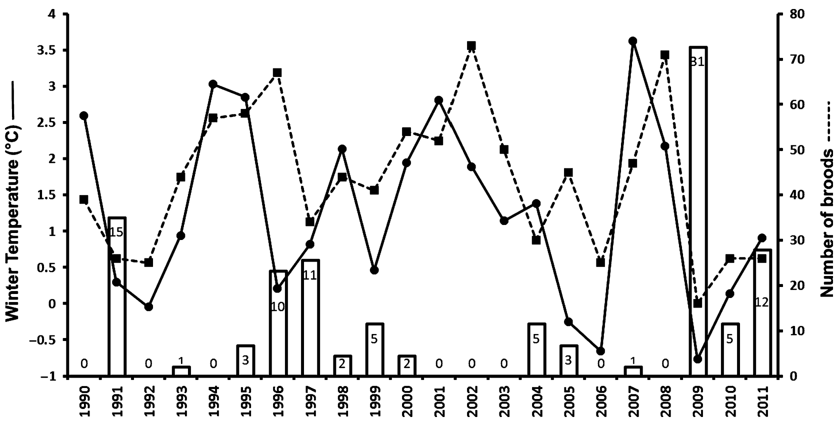

Figure 1. Winter conditions and the number of Barn Owl broods the following breeding season between 1990 and 2011. The number of broods is indicated with a dashed line and the mean winter temperature (°C) with a solid line. Bars indicate the number of days with more than 5 cm of snow cover. Harsher winters coincided with lower brood numbers.

principal components analysis including the proportion of Tawny Owl prey remains that are wood mice, the yearly number of Tawny Owl breeding pairs and their mean annual laying date, clutch size and brood size at fledging (Table 3). The value of the index, hereafter referred to as 'pre-breeding food conditions', increases as breeding conditions improve for the Tawny Owl. The indices of winter severity and pre-breeding food conditions were not significantly correlated (Pearson's $r = -0.30$, $n = 22$ years, $P = 0.17$).

Data analysis

We assessed the effects of pre-breeding food conditions and winter severity on yearly estimates of Barn Owl reproductive parameters for first annual breeding attempts only. Each breeding parameter was entered as a dependent variable in separate linear models. Additional variables that could also influence breeding success were introduced in the models as covariates (i.e. laying date or number of fledglings produced in the study area the year before). Hatching success for the 2011 season was not included in the analyses because we carried out a manipulation of corticosterone in females during egg-laying that might have affected hatching success. Nests that failed during incubation were removed from the hatching success analysis. Analyses of the number of fledglings were performed by only considering pairs that produced at least one fledgling.

Statistical analyses were performed with the software JMP 7.0 (SAS Institute, Cary, NC, USA). Variables were considered significant if the corresponding P-values of two-tailed tests were lower than 0.05. Assumptions for the parametric tests used (homoscedasticity and normal distributions of variables or residuals) were verified in each test. Means are quoted ± 1 se. We did not use stepwise procedures to reduce the number of tests but when doing so during exploratory analyses, we obtained qualitatively similar results. Therefore, full models presented included all the main effects of interest.

RESULTS

Barn Owl population size and laying date

The total number of Barn Owl first clutches per year between 1990 and 2011 ranged from 16 in 2009 to 73 in 2002 (Fig. 1, Table 4). The number of breeding pairs increased with the index of pre-breeding food conditions and was inversely associated with winter severity (Figs 2a and 3a, Table 5). The number of Barn Owl breeding pairs was positively associated with the total number of Barn Owl fledglings produced the year before in the study area (Table 5). Also, Barn Owls started to breed later in years when pre-breeding food conditions were poorer, whereas winter severity did not significantly influence mean laying date (Fig. 2b, Table 5).

We used univariate analyses to measure the extent to which each individual Tawny Owl breeding parameter in Table 1 as well as the

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Table 4. Mean Barn Owl and Tawny Owl reproductive parameters between 1990 and 2011. Range of the yearly mean values as well as the range of individual values is also presented where appropriate. Breeding failure is the number of failed attempts divided by the total number of breeding attempts. Unhatched eggs refers only to eggs that did not hatch for reasons other than the female abandoning her clutch (i.e. unfertile eggs or embryos that died before hatching).

	Barn Owl			Tawny Owl	
	Mean (± se)	Range: annual means	Range: absolute	Mean (± se)	Range: annual means
Number of breeding pairs	43.2 ± 3.4		16–73	41.7 ± 3.3	16–74
Laying date	23 Apr ± 3 days	24 Mar–14 May	25 Feb–5 Aug	2 Mar ± 2 days	15 Feb–19 Mar
Clutch size	5.9 ± 0.1	4.9–6.7	2–11	3.5 ± 0.2	2.6–5.1
Number of unhatched eggs	0.42 ± 0.04	0.14–0.76	0–9	0.18 ± 0.02	0–0.35
Proportion of breeding failure	0.13 ± 0.02	0–0.31		0.25 ± 0.02	0.06–0.44
Number of fledglings	4.22 ± 0.10	3.37–5.08	0–9	3.09 ± 0.16	2–4.33
% *Apodemus* sp. in the diet				58.2 ± 5.2	11.1–89.6

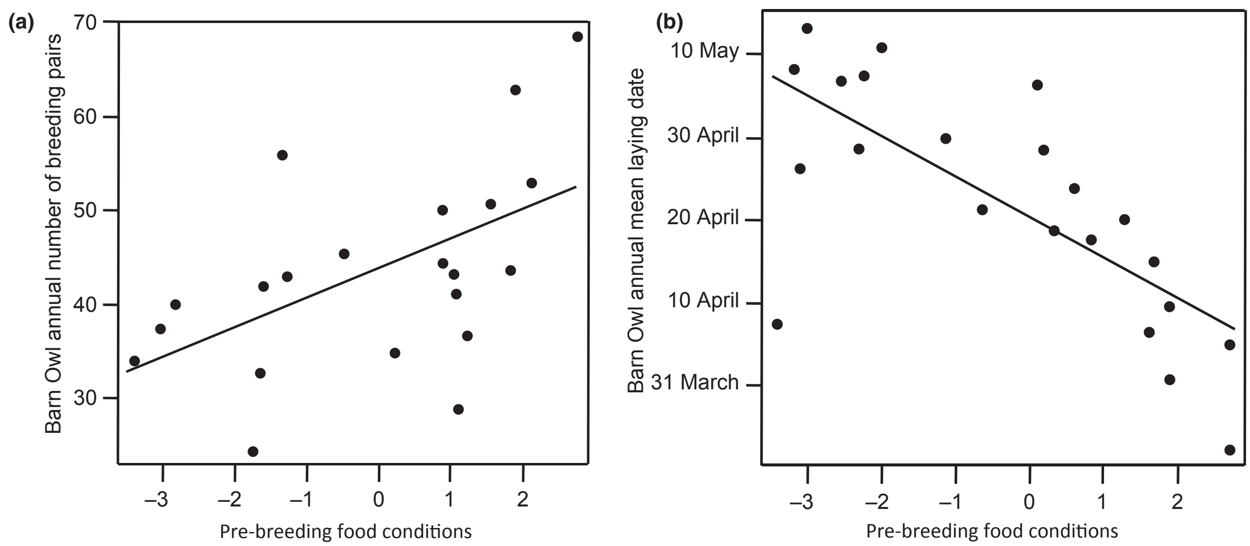

Figure 2. Relationship between an index of pre-breeding food conditions based on Tawny Owl reproductive conditions and (a) the number of Barn Owl breeding pairs (r = 0.54, n = 21 years, P = 0.012, r^2 = 0.28) and (b) annual mean laying date in the Barn Owl (r = –0.72, n = 22 years, P = 0.0002, r^2 = 0.52). The y-values in (a) are leverages that control for the number of fledglings produced the year before and for winter harshness.

proportion of prey remains in Tawny Owl nests that were wood mice were associated with Barn Owl population size and laying date. None of the Tawny Owl parameters was significantly correlated with the number of Barn Owl breeding pairs (Pearson's correlation, $|r| < 0.37$, n = 22 years, $P > 0.09$). Barn Owl laying date was significantly correlated with all Tawny Owl parameters ($|r| > 0.53$, $P < 0.01$) except the proportion of Tawny Owl eggs that did not hatch (r = –0.27, P = 0.23); the strongest association was with Tawny Owl fledging success (r^2 = 0.55; proportion of prey remains that were wood mice, r^2 = 0.34).

Barn Owl clutch size and hatching success

Clutch size was inversely associated with winter severity (Fig. 3b, Table 5) but showed no association with pre-breeding food conditions; the same model showed that clutches were larger in years when Barn Owls bred earlier. Following harsher

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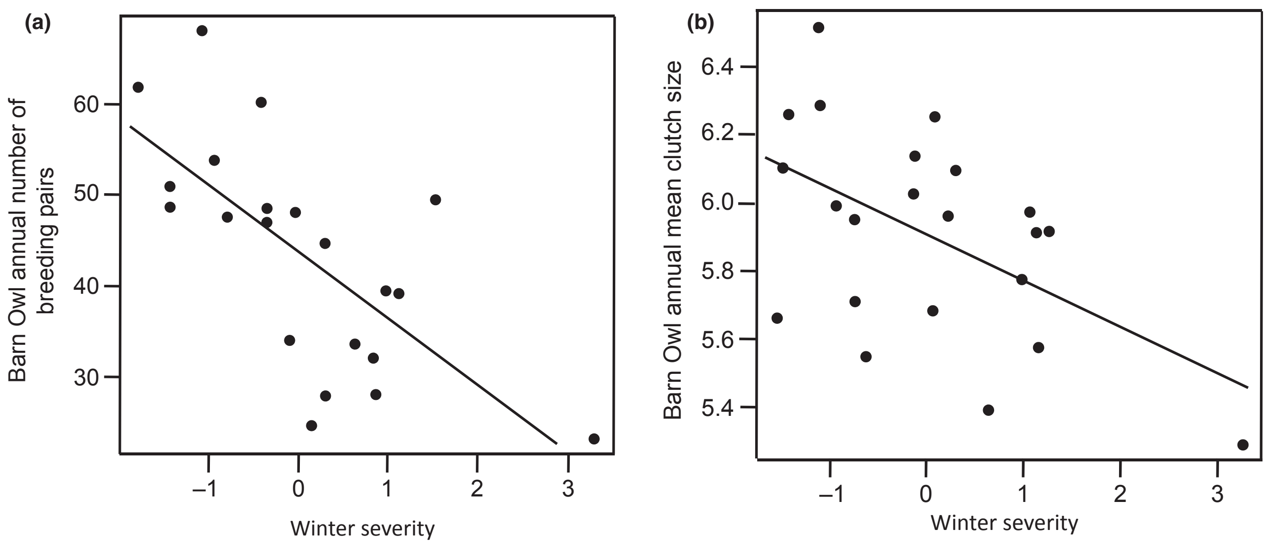

Figure 3. Relationship between an index of winter severity and (a) the number of Barn Owl breeding pairs (Pearson's correlation is $r = -0.69$, $n = 21$ years, $P = 0.0006$; $r^2 = 0.47$) and (b) mean annual clutch size ($r = -0.53$, $n = 22$ years, $P = 0.012$; $r^2 = 0.28$). The *y*-values are leverages that control (a) for the number of fledglings produced the year before and for the pre-breeding food conditions and (b) for laying date effect.

winters, there was a trend towards lower hatching success, whereas pre-breeding food conditions did not explain variation in hatching success (Table 5). Hatching success was unrelated to laying date and clutch size.

Barn Owl breeding success

The number of fledglings in successful broods was related neither to pre-breeding food conditions nor to winter severity (Table 5). The annual proportion of pairs that failed to produce fledglings was not related to pre-breeding food conditions, winter severity or laying date. Total population productivity (total number of fledglings produced by all breeding pairs) was strongly associated with winter severity but not with pre-breeding food conditions or laying date (Table 5).

DISCUSSION

The use of Tawny Owl reproductive parameters as a proxy of pre-breeding food conditions for Barn Owls was well supported. The mean annual proportion of prey remains in Tawny Owl nests that were wood mice was strongly associated with annual variation in the number of Tawny Owl fledglings, percentage of failed nesting attempts, laying date, clutch size, number of breeding couples and hatching success, in order of importance (Table 1). To evaluate the extent to which this index predicts Barn Owl reproductive success, we considered winter severity in the same statistical analyses, as this parameter is already known strongly to affect Barn Owl population dynamics (Schönfeld *et al.* 1977, Chanson *et al.* 1988, Muller 1989, Handrich *et al.* 1993, Marti 1994, Altwegg *et al.* 2003, 2006). Our analyses show that the index of pre-breeding feeding conditions was more strongly associated with Barn Owl laying date than with winter severity, whereas the opposite finding applies to the number of breeding pairs, clutch size and total number of fledglings produced.

Pre-breeding food conditions

As breeding conditions improved for Tawny Owls, Barns Owls started breeding earlier, suggesting that laying date was influenced by pre-breeding food conditions (Fig. 2b). Like Chanson *et al.* (1988), we did not find an association between winter severity and laying date, suggesting that prey abundance before breeding has a greater impact on laying date than does winter severity. In regions characterized by severe winters such as in north-central Utah, laying date seems to be associated with winter snowfall (Marti 1994). This may be a consequence of higher snow cover later into the breeding season, which rarely occurs in our study region.

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Table 5. Linear regression analyses of the relationship between Barn Owl breeding parameters, pre-breeding food conditions and winter severity. Significant (at $P < 0.05$) values are shown in bold. Parameter estimates are given ± 1 se.

Parameter	Variables	Statistical model			Estimate
		d.f.	*F*	*P*	
Breeding pairs	Winter severity	**1,17**	**15.24**	**0.001**	**−7.27 ± 1.86**
	Pre-breeding food conditions	**1,17**	**6.89**	**0.02**	**3.11 ± 1.18**
	Total number of fledglings produced the year before	**1,17**	**13.44**	**0.002**	**0.13 ± 0.04**
Laying date	Winter severity	1,19	0.50	0.49	1.33 ± 1.87
	Pre-breeding food conditions	**1,19**	**18.04**	**0.0004**	**−4.88 ± 1.15**
Mean clutch size	Winter severity	**1,18**	**6.85**	**0.02**	**−0.14 ± 0.05**
	Pre-breeding food conditions	1,18	0.001	0.98	0.001 ± 0.04
	Laying date	**1,18**	**10.56**	**0.004**	**−0.02 ± 0.006**
Hatching success	Winter severity	1,16	2.39	0.14	−0.01 ± 0.006
	Pre-breeding food conditions	1,16	0.27	0.61	0.003 ± 0.007
	Mean clutch size	1,16	0.01	0.92	−0.003 ± 0.02
	Laying date	1,16	0.03	0.86	0.0002 ± 0.0009
Mean annual number of fledglings	Winter severity	1,17	0.63	0.44	−0.06 ± 0.07
	Pre-breeding food conditions	1,17	0.88	0.36	0.05 ± 0.06
	Mean number of hatchlings	1,17	0.07	0.80	−0.07 ± 0.27
	Laying date	1,17	2.75	0.12	−0.02 ± 0.01
Breeding success (proportion of pairs that failed to produce any fledgling)	Winter severity	1,18	0.60	0.45	−0.01 ± 0.01
	Pre-breeding food conditions	1,18	0.27	0.61	0.006 ± 0.01
	Laying date	1,18	0.001	0.98	0.00005 ± 0.002
Total number of fledglings produced	Winter severity	**1,18**	**13.5**	**0.002**	**−29.07 ± 7.91**
	Pre-breeding food conditions	1,18	3.86	0.07	13.14 ± 6.69
	Laying date	1,18	0.27	0.61	−0.50 ± 0.96

The relationship between laying date and pre-breeding food conditions can best be explained through the availability of prey prior to breeding. In the Tawny Owl population, breeding success was strongly influenced by the availability of wood mice (Table 1) and in the early spring, wood mice made up a larger percentage of Barn Owl prey (A. Roulin, unpubl. data) because populations of Common Voles were low at the start of the breeding season (Briner *et al.* 2007, Elmiger *et al.* 2010). The annual percentages of wood mouse remains in Tawny and Barn Owl nests were highly correlated, probably because wood mice were found both in forests where Tawny Owls hunt and in the open landscape where Barn Owls forage. It follows that Tawny Owl breeding parameters and wood mouse prey remains as summarized by the pre-breeding food condition index appear to be a good proxy of food conditions for Barn Owls in early spring.

The fact that clutch size and hatching success were not associated with pre-breeding food conditions suggests that prey abundance has a lower influence than winter severity. Nevertheless, because the index reflects pre-breeding food conditions, we cannot assume that prey availability during the breeding season did not have an impact. It is interesting to note that in our population, as in populations in Scotland (Taylor 1994) and the Netherlands (De Bruijn 1994), clutch size was found to be associated with the same factor (winter severity in our case, and the abundance of voles in the others), as was the number of observed breeders. Marti (1994), however, found that winter severity negatively affected the number of breeding Barn Owls but not clutch size, highlighting that the relative importance of food availability and weather may vary between regions.

Winter severity

Given the growing evidence for climate change and its influence on reproductive success and species distribution (Parmesan 2006), it is crucial to understand weather influences on population dynamics. In species inhabiting high latitudes, winter may be a particularly stressful period. Many studies of birds have found important covariation between winter severity in terms of snow, cold, rainfall and wind, and survival and reproductive

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success (Cawthorne & Marchant 1980, Altwegg *et al.* 2006, Glenn *et al.* 2011). It is therefore critical to take into account the impacts of winter conditions to evaluate the fate of bird populations.

Our results suggest an important impact of winter severity on reproductive parameters in a wild Barn Owl population in western Switzerland. Following milder winters, the number of Barn Owl breeding pairs was higher (Fig. 3a) and clutch size larger (Fig. 3b). The relationships held even when omitting the harshest winter (2009). Negative associations between winter severity and the number of observed breeding individuals have also been shown in Barn Owl studies at high latitudes (North America: Marti & Wagner 1985, Marti 1994; Europe: Baudvin 1986, Altwegg *et al.* 2006). The inverse association with clutch size is in accordance with the results of Baudvin (1986) and could be due to effects on parent body condition through lower prey availability resulting from a deeper snow pack. Although Durant *et al.* (2000) conclude that pre-breeding body condition in Barn Owls does not affect egg production, it is possible that some aspect of female body condition could be affected by harsh winters, which would subsequently influence clutch size and reduce hatching success. For example, winter conditions may affect breeding females through a reduced capacity to carry out the necessary protein metabolism needed for egg production. Breeding females have a higher protein content than non-breeding females and amino acids are critical for egg production (Durant *et al.* 2000). Furthermore, hatching success can be also affected by a female's incubation behaviour, which in turn may be influenced by nutritional state (Smith *et al.* 1989, Mallory & Weatherhead 1993). Harsh weather conditions can negatively affect female body condition, as was observed in the British Isles, where there was a high incidence of clutches with unhatched eggs when high rainfall reduced male food provisioning (Shawyer 1987).

Fledging success

There was no association between either pre-breeding food conditions or winter severity, and the number of fledglings in individual Barn Owl broods, as also found by Marti (1994). The lack of association may be due to the fact that the winter period, as defined in our study, ends approximately 5 months before the mean fledging date. Barn Owls may therefore have enough time to compensate for any effects of winter on body condition, and rodent populations may have had enough time to increase to sufficient levels. Instead, climatic conditions during the rearing period could play a more important role in influencing fledging success.

In conclusion we show that, alongside measures of winter severity, Tawny Owl reproductive performance and diet are strongly associated with Barn Owl laying date and breeding population size. Weather conditions prevailing in winter and during reproduction (Chausson *et al.* 2014) therefore have a strong impact on Barn Owl reproductive success in Switzerland.

More generally, our work shows that aspects of the ecology and demography of one species can be used in some circumstances as a bio-indicator of the quality of the environment for a related species of similar ecology.

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