Factors Affecting Timing of Breeding in the Tawny Owl *Strix aluco*

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Abstract: Relevant variables characterising factors suspected to affect timing of breeding in birds may be difficult to measure. Then, easily available proxies, i.e. variables that are expected to vary consistently with some affecting factors, may be used instead. In the present study on tawny owls, I used besides individual characteristics of parent birds both detailed measurements of the prey base of territories, local and general indices of vole abundance as well as local and general weather conditions as explanatory variables. Owls tended to breed the earlier the older and the heavier they were. Breeding was the earlier the higher the abundance of water voles and the proportion of field voles in the territorial prey samples. Owls bred earlier when the local abundance of small voles in the preceding autumn was high. Regional vole indices showed no associations with timing of owls' breeding. Single winter weather variables did not show any significant associations neither. In combination with the advancing effect of water vole abundance, however, the delaying effect of the depth of the snow cover in March was significant. Models based on different data sets showed different kinds of associations between the abundance of small voles and timing of breeding in owls. The best models in which both intrinsic and extrinsic explanatory variables (characteristics of parent birds and environmental factors, respectively) were included did not differ considerably from each other. The occurrence of water voles in prey samples governed the best models. The results suggest, that without detailed knowledge on the prey base of territory, misleading results may emerge and the importance of small voles in governing breeding of owls may be overemphasised.

Keywords: Extrinsic factors, fixed effects, intrinsic factors, local prey, random effects, regional vole indices, winter weather variables.

INTRODUCTION

The onset of breeding in birds is governed by various intrinsic and extrinsic factors, including individual characteristics of parent birds and prevailing environmental conditions, in particular food supply, respectively [1-4]. The early onset of breeding has been suggested as a favourable trait that evolved to ensure the best feeding conditions for the forthcoming young [e.g. 1]. In various long-lived species of northern latitudes early breeding is important to ensure that the time-consuming reproduction process can be conducted within the strict limits of tolerable environmental conditions and for young birds to successfully reach independence [5-7]. Early breeding may also offer the opportunity to produce more clutches and young within a season [e.g. 2].

Determining timing of breeding on the basis of direct observations during the egg laying is a relatively easy task if there is no risk of desertion of the clutch. Particularly convenient it is on the basis of age of nestlings if it can be determined by some measurement of growth. Measuring meaningful variables characterising intrinsic and extrinsic factors suspected to affect timing of breeding may, however, be more complicated, and this may restrict the sample size available. For instance, detailed observation and measurement of individual characteristics of parent birds requires live-catching of birds that may be impractical or difficult to conduct. Relevant characteristics of territory, including the prey base during the pre-laying period may be very laborious to determine with the precision needed. In such cases, more easily available indirect measurements may be used as proxies, i.e. as variables that are expected to vary consistently with some affecting factors. Their capability to predict the effects considered, however, vary and may be quite restricted.

In the present study, I examined the role of some intrinsic and extrinsic factors in timing of breeding in the tawny owl *Strix aluco* (Linnaeus 1758) in southern Finland. This species has an advantage to allow gathering various kinds of relevant data with relative ease. For instance, artificial nest sites of the species are easily accessible, breeding adults are quite easy to catch from nests, and prey used can be analysed from the remains in the nest bottom litter samples [e.g. 8-10]. So, in addition to general indices of food abundance and weather conditions, I also used individual characteristics of parent birds and detailed measurements of territorial prey base as explanatory variables. My aim was not only to evaluate some expectations of associations between variables but also to demonstrate effects of sample size, different data sets, and various proxies of explanatory variables on the results and conclusions derived.

My expectations were as follows (Fig. **1**): 1) Being more competent in reproduction [9], older individuals might also be more competent being capable to breed earlier than younger ones [e.g. 11, 12]. Birds that are smaller-sized [13, 14] but heavier, and thus probably in better condition [15, 16], should breed earlier than larger but lighter ones. 2) High prevalence of voles (peaks of vole cycles, good availability

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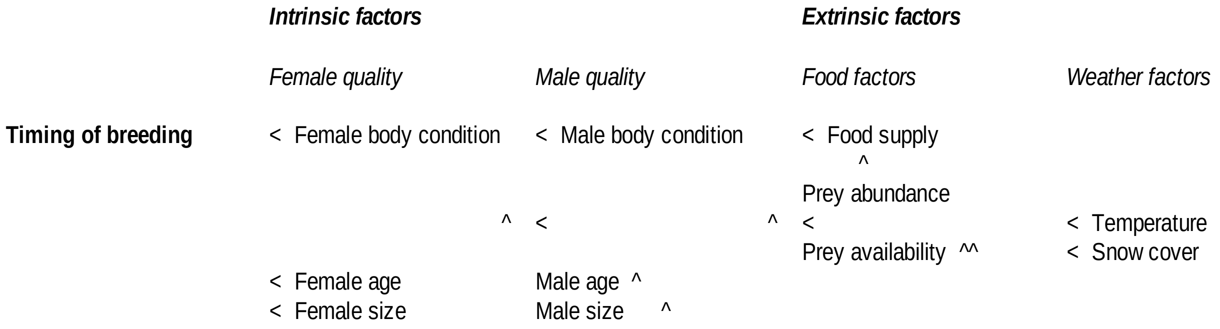

Fig. (1). A conceptual model for the links between different factors expected to affect the timing of breeding in the tawny owl *Strix aluco* in southern Finland.

due to minor snow) and rats (permanent local food source) in the prey base of territory should be associated with early breeding, corresponding to their relationship with reproduction [8]. Abundance of water voles *Arvicola amphibius* (Linnaeus 1758) should be important particularly in combination with minor snow cover [8, 10]. 3) High general abundance of small voles and mild and less snowy conditions of the preceding winter should have an advancing effect on breeding of owls [e.g. 2, 17]. Compared to territorial and individual variables, however, the explanatory power of regional vole indices and general weather variables may be rather weak and insignificant, particularly in small samples.

MATERIAL AND METHODS

The tawny owl is a widespread bird of prey of rural and urban habitats in Europe [18, 19]. It commonly occupies habitats in the vicinity of human settlements. A suitable nesting cavity is an essential prerequisite for the tawny owl's breeding, which is otherwise largely governed by adequate availability of food [e.g. 8, 10, 20]. In the North, the availability of food for breeding tawny owls seems to be particularly affected by the pronounced and more or less cyclic fluctuations of vole populations [21-24] and it is modified by habitat [25, 26] and various climatic factors [8, 20, 22, 27, 28].

Population Study and Study Area

The present data were derived from a ten-year period (between 1989 and 1999) of a long-term study on population dynamics of the tawny owl conducted in Uusimaa (60°N, 25°E), near the southern coast of Finland [8]. The study area of more than 500 km^2 consisted of low-lying rural habitats of mixed fields and forests, as well as more urban environments of the capital Helsinki and its surroundings. Tawny owls occupied the study area in a relatively even manner, following the availability of suitable nest sites, mainly nest boxes erected throughout the study area. The hatching success of birds was recorded for each year of the study. Only the successfully hatched clutches were included in the present data because the timing of breeding was determined on the basis of the hatching date.

Determination of the Hatching Date

In order to estimate the hatching dates, I measured the wing length of nestlings from 193 broods using the maximum method [e.g. 29]. I estimated the age of the oldest young using Jokinen's [30] wing growth curve. The hatching dates were estimated from the age of the young. For the timing of egg laying, I used an incubation time of 28 days [19]. Calendar days were converted to Julian days, starting from the first day of January.

Explanatory Variables

Intrinsic Factors

Breeding tawny owls (females and males) of the population were captured at nests by hoop net or trap around the middle of the nestling period. Due to the well-known risk of desertion of nest in the early phases of breeding in the tawny owl [9], catchings were not performed earlier. Captures occurred mainly in May, but were distributed from March to June. Each individual was captured only once during each breeding season. The total data included 193 breeding pairs.

Birds were sexed on the basis of their size, wing length, body mass and the prominent incubation patch of the females [9, 20, 31]. I determined the age of birds by the plumage patterns [32]. The three age categories used included 1 yr old, 2 yrs old, and 3 yrs old or older birds. The maximum wing length, i.e., the distance between the carpal joint and the tip of the longest primary [29], indicated the size of an individual. The body mass (measured by Pesola spring balance to the nearest gram) was used as a measure of body condition [33]. Within sex, the explanatory variables were usually correlated. The annual values of male and female body mass were also significantly correlated ($r = 0.417$, $df = 87$, $P < 0.001$).

Food Variables

Local prey of tawny owls during the breeding season was studied by analysing 51 nest bottom litter samples collected after breeding from 30 different locations (local nesting territories) [34]. The samples represented both good (33) and poor (18) vole years. Food remains (bones, feathers etc.) were separated from the litter by picking with tweezers. They were assorted and identified in appropriate categories [8]. In each prey category, the number of individuals was counted on the basis of the most common individual bones found. The identification of mammals was based mainly on jawbones (mandibles) and bones of limbs, including hipbones, femurs, tibiae, and humeri. Birds were recognised based on limb-bones (femurs, tibio-tarsi, tarso-metatarsi, humeri, ulnae, metacarpals) as well as sternums, beaks, and feathers. The numbers and proportions of different species of voles in samples were significantly correlated ($P < 0.05$).

The species of small voles that were considered to form an important food source for owls and the abundance of which was estimated on the basis of local and regional snap-trappings were the bank vole *Myodes glareolus* (Schreber 1780) and the field vole *Microtus agrestis* (Linnaeus 1761). The catch indices were expressed as individuals per 100 trap-nights. General fluctuations of the vole populations within the study area were monitored by small-scale trapping, catch indices of which are here called "local vole indices". In a central locality (Sipoo, Hindsby), small mammals were trapped in each autumn (October–November) and spring (May) at 30 standard points along a line of about 1.5 km with three snap-traps at each point (total of 90 traps) throughout a 24-hour period. On the basis of the vole index of the preceding autumn, the study years of the breeding seasons were classified as “good” or “poor” ones, corresponding to good and poor vole years in the three-year vole cycles. From the point of view of tawny owls, the habitat distribution of the trapping line might have been concentrated in forests, but old fields were also included. However, the proportions of forest and open habitat seemed roughly to correspond to those of the district at large.

In order to characterise the general abundance of food for owls before breeding season, I used regional small vole indices of the preceding autumn and current spring. Each index was based on a total of 384 trap-nights of trappings conducted during two-day periods in early October and May in two localities near the present study area and they included both forest and old field habitats, 192 trap-nights each [Kimpari Bird Projects, 24, 35]. These indices seemed to characterise fluctuations in the abundance of voles over a larger area in southern Finland relatively well [22, 24].

Weather Variables

I examined effects of the local mean temperature of winter, including January, February and March, as well as the depth of the snow cover in the middle of March (Finnish Meteorological Institute). These variables seemed to characterise well the strength of winter before the breeding season of tawny owls. For characterising the weather conditions at large, I applied the winter index of the North Atlantic oscillation (NAO), which is the most prominent pattern of atmospheric variability over the northern hemisphere and which has a marked effect on European weather conditions [36, 37]. The increasing positive values of the winter NAO indices, averaging the monthly values from December to March (http://www.cru.uea.ac.uk/cru/data/nao.htm [accessed 23 March 2011]), indicate milder and wetter winter weathers in Europe.

Preliminary examination of the data showed that there was a significant negative correlation between the mean winter temperature and the depth of the snow cover in March ($r = -0.664$, $df = 9$, $P = 0.013$). There was a significant positive correlation between the winter NAO index and local mean temperature of winter ($r = 0.744$, $df = 9$, $P = 0.004$) whereas the relationship between the winter NAO index and the depth of the snow cover in March was only nearly significant ($r = -0.485$, $df = 9$, $P < 0.065$).

Data Sets Used

The material used consisted of three smaller sets of data on tawny owls: 1) nestings from which both the hatching date was determined and each parent bird was caught and examined (N = 89), 2) nestings from which both the hatching date was determined and prey remains were analysed (N = 42), and 3) nestings from which the hatching date was determined, each parent bird was caught and examined, and prey remains were analysed (N = 21). Thus, in different analyses, the numbers and combination of variables somewhat varied.

Statistics

In searching for the factors affecting timing of breeding in the tawny owl, I used linear mixed effects models (lme) [38] from nlme in R statistical package [39, 40]. In the analyses, I used the Julian hatching date of the oldest young in the brood as the response variable. The explanatory variables (fixed effects) included the age, wing length and body mass of the parent birds (intrinsic factors) as well as various food and weather indices (extrinsic factors). The territorial food indices included the numbers or proportions of small voles (field voles and bank voles both separately and combined), water voles, rats, mice, shrews, and birds in the prey remains of the nest bottom litter samples. In separate models, local and regional autumn and spring vole indices based on snap-trappings of small voles were used. Weather variables included the mean temperature of the preceding winter, depth of the snow cover in March and the winter NAO index. Due to the common correlation between variables, largely only separate effects of variables were considered. The territory ID, indicating unknown local impacts, and year, indicating annually varying unknown factors, characterised random effects. The models used had a general appearance as follows: Hatching date model <- lme (Hatching date ~ Fixed effects, Random effects ~ Territory ID * Year). The fixed effects were fit into the model as single variables or in reasonable combinations of variables, following the expectations issued (Fig. **1**). The significance of variables in each model was examined and the models were ranked on the basis of the Akaike Information Criterion (AIC) [41, 42].

RESULTS

Older birds tended to breed earlier than younger ones (Table **1**). This concerned particularly females. Large body size was associated with early breeding in females but not in males. Birds that were heavy and in good body condition bred earlier than lighter and less fit individuals. The combining of male and female chracteristics did not make the models better.

The breeding of owls was the earlier, the higher the number of water voles and the proportion of field voles in the territorial prey samples (Table **2**). The occurrence of rats showed no such association. The proportion of shrews was higher in the prey samples of late nestings.

Owls bred earlier when the local vole levels in the preceding autumn were high (Table **3**). There were no significant associations between the regional vole indices and timing of breeding of owls.

Table 1. Fixed Effects of Age, Size (Wing Length) and Condition (Body Mass) of Parent Birds on Timing of Breeding in the Tawny Owl *Strix aluco* in Southern Finland Based on Linear Mixed Effects Models (Hatching Date ~ Factor, Random Effects [Territory ID, Year]). The Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t), Probabilities (p) and Akaike's Information Criterions (AIC) Are Given. In Each Model, the Number of Observations Is 89 and Number of Groups (Years) 10. Negative Relationships Suggest Advancing Effects

Parent	Fixed effects	Value	SE	df	*t*	*p*	AIC
Female	(Intercept)	131.031	6.352	78	20.630	<0.001	740.446
	Age	-4.158	1.948	78	-2.134	0.036	
Female	(Intercept)	382.514	73.658	78	5.193	<0.001	737.082
	Wing length	-0.870	0.244	78	-3.563	<0.001	
Female	(Intercept)	167.065	14.996	78	11.141	<0.001	743.838
	Body mass	-0.082	0.026	78	-3.202	0.002	
Male	(Intercept)	132.608	7.689	78	17.247	<0.001	741.065
	Age	-4.556	2.452	78	-1.858	0.067	
Male	(Intercept)	178.771	79.235	78	2.256	0.027	748.284
	Wing length	-0.203	0.275	78	-0.738	0.463	
Male	(Intercept)	193.627	22.130	78	8.750	<0.001	741.656
	Body mass	-0.173	0.052	78	-3.351	0.001	

Winter weather variables, in general, showed at their best only nearly significant associations with the timing of owls' breeding (Table **4**). In combination with the advancing effect of water vole abundance, however, the delaying effect of the depth of the snow cover in March was significant. Nevertheless, the addition of the snow cover did not make the model better (AIC 322.795 > 321.290).

Models based on different data sets showed different kinds of associations between the abundance of small voles and timing of breeding in tawny owls (Table **5**). Significant associations emerged particularly in the smallest data sets of various prey samples. In a larger data set, the local vole indices of the preceding autumn also showed a significant relationship with the hatching date of owls while none of the regional vole indices showed such an association.

The best models in which both intrinsic and extrinsic explanatory variables were included did not differ considerably from each other (AICs were relatively similar) (Table **6**). The only significant factor, the occurrence of water voles in the prey remains of the nest bottom litter samples, governed the best models. In addition, male body mass and the winter NAO index were included in several of the best models.

DISCUSSION

In the mixed effects models constructed, the prevalence of water voles in the local prey base seemed to be the most important single factor affecting timing of breeding in the tawny owl population studied. Occurrence of smaller-sized species of voles also seemed to be of considerable importance. Detection of these associations seemed to depend largely on the capability of the proxies used as explanatory variables to characterise the underlying factors.

Intrinsic Factors

As expected, older birds, in particular females, tended to breed earlier than younger ones. This seemed to be a common phenomenon in birds [11, 12] but not a universal one even in the tawny owl [see 7]. Large body size in early-breeding females was against some earlier findings [e.g. 13, 14]. High body mass, indicating good body condition, was a good indicator of early breeding in both sexes. This is suggested particularly for female birds also in various earlier studies [15, 16, 43].

Local Prey Base

The prey samples representing single local territories showed clearly the importance of the occurrence of voles, in particular water voles, in timing of breeding in the tawny owl population studied. High prevalence of voles, suggesting peak years in the vole cycles or good availability of voles due to minor snow cover, seem to be a common prerequisite for early breeding in owls [e.g. 2, 10].

Occurrence of rats in the prey base of territories did not show the expected advance in breeding in the present data. This might be due to an uneven distribution of rat concentrations of the study area and the small number of nest samples analysed. High proportion of shrews in late nests refers rather to lack of voles than to some direct effect of shrews in owls' diet.

Fluctuations in Vole Abundance

Abundance fluctuations of small voles did not only reflect in the prey base of territories but also in the local and regional vole catch indices. The association between the regional indices and timing of breeding in the tawny owl

Table 2. **Associations Between the Indices of Single Species or Categories of Territorial Prey Base (Abundance [A] and Proportion [%] of Individuals of Prey Categories in Remains Identified from the Nest Bottom Litter Samples) and Timing of Breeding (Julian Hatching Date of the Oldest Young in the Brood) in the Tawny Owl *Strix aluco* in Linear Mixed Effects Models (Hatching Date ~ Prey Index, Random Effects [Territory ID, Year]). The Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t), Probabilities (p) and Akaike's Information Criterions (AIC) Are Given. In Each Model, the Number of Observations Is 42 and Number of Groups (Years) 10. Negative Relationships Suggest Advancing Effects**

Fixed effects	Value	SE	df	*t*	*p*	AIC
(Intercept)	120.799	3.154	31	38.301	<0.001	328.747
Field voles A	-0.267	0.162	31	-1.647	0.110	
(Intercept)	119.447	3.576	31	33.404	<0.001	328.516
Bank voles A	-0.253	0.539	31	-0.468	0.643	
(Intercept)	120.757	3.263	31	37.006	<0.001	329.688
Small voles A	-0.191	0.132	31	-1.454	0.156	
(Intercept)	123.070	2.910	31	42.294	<0.001	322.795
Water voles A	-0.768	0.255	31	-3.010	0.005	
(Intercept)	117.412	3.532	31	33.242	<0.001	326.931
Rats A	0.767	0.959	31	0.801	0.429	
(Intercept)	116.609	3.821	31	30.517	<0.001	328.798
Mice A	0.314	0.332	31	0.947	0.351	
(Intercept)	117.468	3.405	31	34.495	<0.001	329.437
Shrews A	0.226	0.217	31	1.043	0.305	
(Intercept)	117.074	4.030	31	29.050	<0.001	330.034
Birds A	0.148	0.224	31	0.662	0.513	
(Intercept)	124.827	3.383	31	36.901	<0.001	325.261
Field voles %	-0.486	0.177	31	-2.752	0.010	
(Intercept)	117.594	4.069	31	28.900	<0.001	328.817
Bank voles %	0.227	0.451	31	0.504	0.618	
(Intercept)	125.695	3.910	31	32.144	<0.001	326.941
Small voles %	-0.397	0.164	31	-2.429	0.021	
(Intercept)	127.344	2.581	31	49.337	<0.001	312.443
Water voles %	-0.917	0.176	31	-5.220	<0.001	
(Intercept)	119.269	3.729	31	31.988	<0.001	328.207
Rats %	-0.203	0.661	31	-0.306	0.761	
(Intercept)	114.637	3.933	31	29.146	<0.001	328.204
Mice %	0.327	0.206	31	1.585	0.123	
(Intercept)	114.513	3.536	31	32.381	<0.001	324.359
Shrews %	0.551	0.216	31	2.554	0.016	
(Intercept)	113.718	4.171	31	27.264	<0.001	328.544
Birds %	0.222	0.125	31	1.773	0.086	

Table 3. Associations Between the Indices of Local and Regional Autumn and Spring Abundance of Small Voles (*Microtus, Myodes*) and Timing of Breeding (Julian Hatching Date of the Oldest Young in the Brood) in the Tawny Owl *Strix aluco* in Linear Mixed Effects Models (Hatching Date ~ Vole Index, Random Effects [Territory ID, Year]). The 'Mean' Indices Are Averages Between Autumn and Spring. The Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t), Probabilities (p) and Akaike's Information Criterions (AIC) Are Given. In Each Model, the Number of Observations is 89 and Number of Groups (Years) 10. Negative Relationships Suggest Advancing Effects

Model	Fixed effects	Value	SE	df	*t*	*p*	AIC
Local autumn	(Intercept)	132.045	5.392	79	24.488	<0.001	742.619
	Small voles	-1.080	0.412	8	-2.620	0.031	
Local spring	(Intercept)	123.398	5.260	79	23.459	<0.001	742.710
	Small voles	-3.497	4.029	8	-0.868	0.411	
Regional autumn	(Intercept)	128.272	7.996	79	16.043	<0.001	745.074
	Small voles	-1.072	0.949	8	-1.129	0.292	
Regional spring	(Intercept)	133.186	11.064	79	12.038	<0.001	741.200
	Small voles	-7.210	5.847	8	-1.233	0.253	
Regional mean	(Intercept)	131.466	9.174	79	14.330	<0.001	743.283
	Small voles	-2.428	1.827	8	-1.328	0.221	
Regional autumn	(Intercept)	123.510	5.930	79	20.827	<0.001	744.377
	Field voles	-1.428	1.995	8	-0.716	0.494	
Regional spring	(Intercept)	119.648	6.538	79	18.301	<0.001	742.787
	Field voles	0.867	5.753	8	0.151	0.884	
Regional mean	(Intercept)	125.519	7.968	79	15.752	<0.001	742.710
	Field voles	-3.346	4.492	8	-0.745	0.478	
Regional autumn	(Intercept)	127.818	7.956	79	16.065	<0.001	744.514
	Bank voles	-1.434	1.338	8	-1.072	0.315	
Regional spring	(Intercept)	128.263	6.387	79	20.082	<0.001	740.462
	Bank voles	-8.890	5.871	8	-1.514	0.168	
Regional mean	(Intercept)	129.803	8.208	79	15.814	<0.001	742.827
	Bank voles	-3.103	2.394	8	-1.296	0.231	

population studied was, however, not significant [cf. also 10]. For a larger data set and a longer period of time, however, a significant association emerged [17]. This suggests that there is considerable spatial and temporal variation in the general pattern of vole cycles, in spite of the fact that the cycles may be in a similar general phase over a large spatial scale [23, 27, 44].

Winter Weather

In general, the effects of winter weather on timing of breeding in owls seemed to be minor. In any case, these effects should be largely indirect [22, 24]. This is suggested also by the relationships between the snow cover, occurrence of water voles, and hatching date of owls in the present study. Correspondingly, the finding that birds that were heavy and in good body condition bred earlier than other individuals suggests that winter weather conditions may be involved by affecting the availability of small voles that, in turn, could be responsible for good body condition of overwintering owls. However, the adding of snow cover along with a measure of water vole occurrence into the model seems not make it better.

Effects of Quality and Quantity of Data

For practical reasons, I generally used various indirect measures as proxies of variables in the mixed effects models. The onset of breeding was characterised by the hatching date estimated on the basis of age characterised by the wing length of the oldest young when the nestlings of the brood were ringed. The size of owls was characterised by the wing length. The condition of parent birds *before* breeding was characterised by the body mass *during* breeding. The prey base of territories *before* breeding was characterised by the remains analysed from the nest bottom litter samples

Table 4. **Effects of Weather and Vole Abundance on Timing of Breeding in the Tawny Owl *Strix aluco* in Southern Finland Based on Linear Mixed Effects Models (Hatching Date ~ Fixed Effects, Random Effects [Territory ID, Year]). Weather Variables Included Mean Winter Temperature, Snow Cover in March and Winter NAO Index. Vole Indices Included Water Vole Abundance (A) and Proportion (%) in the Nest Bottom Litter Samples as well as Regional Small Vole Index in Spring. The Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t), Probabilities (p), Akaike's Information Criterions (AIC) and Numbers of Observations (N) Are Given. Negative Relationships Suggest Advancing Effects**

Fixed effects	Value	SE	df	*t*	*p*	AIC	N
(Intercept)	118.168	3.338	31	35.400	<0.001	321.290	42
Snow cover	0.406	0.171	8	2.374	0.045		
Water voles A	-0.679	0.248	31	-2.740	0.010		
(Intercept)	118.113	3.462	30	34.121	<0.001	328.142	42
Snow cover	0.418	0.226	8	1.850	0.101		
Water voles A	-0.673	0.268	30	-2.510	0.018		
Snow cover:Water voles A	-0.003	0.035	30	-0.088	0.930		
(Intercept)	123.409	3.443	31	35.839	<0.001	313.503	42
Snow cover	0.266	0.158	8	1.682	0.131		
Water voles %	-0.797	0.185	31	-4.300	<0.001		
(Intercept)	122.604	3.559	30	34.454	<0.001	319.822	42
Snow cover	0.412	0.216	8	1.905	0.093		
Water voles %	-0.716	0.201	30	-3.559	0.001		
Snow cover:Water voles %	-0.028	0.028	30	-0.989	0.331		
(Intercept)	112.814	6.811	79	16.564	<0.001	743.300	89
Mean winter temperature	-2.414	1.814	8	-1.330	0.220		
(Intercept)	113.852	4.964	79	22.937	<0.001	745.683	89
Snow cover	0.511	0.280	8	1.825	0.106		
(Intercept)	125.633	4.337	79	28.970	<0.001	740.734	89
Winter NAO	-5.016	2.521	8	-1.990	0.082		
(Intercept)	126.261	11.303	79	11.171	<0.001	738.029	89
Mean winter temperature	-2.621	1.719	7	-1.525	0.171		
Regional spring small voles	-7.919	5.481	7	-1.445	0.192		
(Intercept)	118.854	23.313	79	5.098	<0.001	735.837	89
Mean winter temperature	-4.276	4.801	6	-0.891	0.407		
Regional spring small voles	-2.986	14.603	6	-0.204	0.845		
Winter temperature:Spring voles	1.155	3.117	6	0.370	0.724		
(Intercept)	130.696	8.471	79	15.429	<0.001	738.280	89
Snow cover	0.651	0.238	7	2.740	0.029		
Regional spring small voles	-10.408	4.550	7	-2.288	0.056		
(Intercept)	118.925	14.288	79	8.323	<0.001	739.196	89
Snow cover	1.388	0.767	6	1.809	0.120		
Regional spring small voles	-3.263	8.336	6	-0.391	0.709		

(Table 4) contd….

Fixed effects	Value	SE	df	*t*	*p*	AIC	N
Snow cover:Spring voles	-0.418	0.414	6	-1.010	0.352		
(Intercept)	133.547	10.168	79	13.134	<0.001	736.736	89
Winter NAO	-4.438	2.648	7	-1.676	0.138		
Regional spring small voles	-4.768	5.529	7	-0.862	0.417		
(Intercept)	134.430	9.892	79	13.590	<0.001	732.456	89
Regional spring small voles	-7.583	5.883	6	-1.289	0.245		
Winter NAO	-11.555	6.720	6	-1.720	0.136		
Winter NAO:Spring voles	5.519	4.807	6	1.148	0.295		

Table 5. Effects of the Abundance of Small Voles on Timing of Breeding in the Tawny Owl *Strix aluco* on the Basis of Mixed Effects Models (Hatching Date ~ Fixed Effects [Small Vole Abundance], Random Effects [Territory ID, Year]) with Various Local and Regional Vole Indices and Data Sets of Different Size. The 'Mean' Indices Are Averages Between Autumn and Spring. The Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t), Probabilities (p), Akaike's Information Criterions (AIC) as well as Numbers of Observations (N) and Years (Y) in Each Model Are Given

Index/Data	Fixed effects	Value	SE	df	*t*	*p*	AIC	N	Y
Territorial/small	(Intercept)	127.190	4.260	12	29.860	<0.001	159.343	21	8
	Field voles in prey	-0.574	0.177	12	-3.250	0.007			
Territorial/medium	(Intercept)	120.790	3.154	31	38.301	<0.001	328.747	42	10
	Field voles in prey	-0.267	0.162	31	-1.647	0.110			
Regional/small	(Intercept)	128.508	5.192	13	24.750	<0.001	159.216	21	8
	Autumn field voles	-4.908	2.381	6	-2.061	0.085			
Regional/large	(Intercept)	123.510	5.930	79	20.827	<0.001	744.377	89	10
	Autumn field voles	-1.428	1.995	8	-0.716	0.494			
Regional/small	(Intercept)	120.578	7.596	13	15.873	<0.001	161.048	21	8
	Spring field voles	0.596	6.394	6	0.093	0.929			
Regional/large	(Intercept)	119.648	6.538	79	18.301	<0.001	742.787	89	10
	Spring field voles	0.867	5.753	8	0.151	0.884			
Regional/large	(Intercept)	125.519	7.968	79	15.752	<0.001	742.710	89	10
	Mean field voles	-3.346	4.492	8	-0.745	0.478			
Territorial/small	(Intercept)	125.889	4.499	12	27.983	<0.001	160.576	21	8
	Bank voles in prey	-1.606	0.703	12	-2.283	0.041			
Regional/small	(Intercept)	125.585	8.841	13	14.204	<0.001	163.473	21	8
	Autumn bank voles	0.935	1.554	6	-0.602	0.569			
Regional/large	(Intercept)	127.818	7.956	79	16.065	<0.001	744.514	89	10
	Autumn bank voles	-1.434	1.338	8	-1.072	0.315			
Regional/small	(Intercept)	128.056	7.626	13	16.792	<0.001	159.618	21	8
	Spring bank voles	-7.492	6.631	6	-1.130	0.302			
Regional/large	(Intercept)	128.263	6.387	79	20.082	<0.001	740.462	89	10
	Spring bank voles	-8.890	5.871	8	-1.514	0.168			

(Table 5) contd….

Index/Data	Fixed effects	Value	SE	df	*t*	*p*	AIC	N	Y
Territorial/small	(Intercept)	126.732	4.284	11	29.584	<0.001	157.863	21	8
	Field voles in prey	-0.922	0.408	11	-2.262	0.045			
	Bank voles in prey	1.376	1.450	11	0.949	0.363			
Regional/large	(Intercept)	129.803	8.208	79	15.814	<0.001	742.827	89	10
	Mean bank voles	-3.103	2.394	8	-1.296	0.231			
Territorial/small	(Intercept)	127.097	4.303	12	29.534	<0.001	160.478	21	8
	Small voles in prey	-0.441	0.143	12	-3.084	0.010			
Local/large	(Intercept)	132.045	5.392	79	24.488	<0.001	742.619	89	10
	Autumn small voles	-1.080	0.412	8	-2.620	0.031			
Local/large	(Intercept)	123.398	5.260	79	23.459	<0.001	742.710	89	10
	Spring small voles	-3.497	4.029	8	-0.868	0.411			
Regional/small	(Intercept)	130.565	8.617	13	15.153	<0.001	162.745	21	8
	Autumn small voles	-1.495	1.171	6	-1.277	0.249			
Regional/large	(Intercept)	128.272	7.996	79	16.043	<0.001	745.074	89	10
	Autumn small voles	-1.072	0.949	8	-1.129	0.292			
Regional/small	(Intercept)	133.935	13.313	13	10.061	<0.001	159.788	21	8
	Spring small voles	-6.986	6.813	6	-1.025	0.345			
Regional/large	(Intercept)	133.186	11.064	79	12.038	<0.001	741.200	89	10
	Spring small voles	-7.210	5.847	8	-1.233	0.253			
Regional/large	(Intercept)	131.466	9.174	79	14.330	<0.001	743.283	89	10
	Mean small voles	-2.428	1.828	8	-1.328	0.221			

after breeding. Fluctuations in the general level of the food supply *before* breeding were described by the catch indices of local and regional snap-trappings in the preceding autumn or next spring. Climatic effects were depicted by single local or regional measures of the mean temperature of winter and the depth of the snow cover as well as the global winter indices of the North Atlantic oscillation.

Variation in the explanatory power of variables can be demonstrated by subsamples of larger data sets or by using corresponding data sets of different origin as replicates. In the present case, the samples were selected on the basis of the availability of required variables in each subsample. In addition, effects of vole abundance were examined based on the indices derived from sources of three spatial scales. Various differences emerged. Not surprisingly, in general, the local variables seemed to have a stronger association with the response variable than the regional ones. Larger samples from a data set did not always perform better than smaller ones, indicating that the real total variation in the variables concerned may be considerable.

Large differences emerged in the associations between subsamples of different size suggest that between territories there were also considerable differences other than those concerning the prey base and that were revealed by the remains in the nest bottom litter. These differences were sealed within the random effects in form of the territory IDs in the mixed effects models.

The Best Models

Several of the best models characterising the effects governing timing of breeding in tawny owls performed roughly equally with each other. This was probably due to the fact that the one and only significant factor, the occurrence of water voles, overwhelmingly governed the models and effectively outweighed the impact of other factors [cf. 9, 10]. Detailed ranking of the best models seems, however, not necessarily relevant or even reasonable if the proxies used poorly represent the variables intended. So, also the importance of the effects of single explanatory variables may be difficult to estimate [cf. e.g. 42]. Without an experimental approach, in such situations we can only state that there is or is not a significant association between the explanatory and response variables of the model.

CONCLUSIONS

Mixed effects models of a single fixed effect may give indications of importance of single variables. In models of two or more fixed effects, a governing factor, in the present

Table 6. A Compilation of the Best Mixed Effects Models of the Associations of Characteristics of Parent Birds, Local Prey (Abundance [A] or Proportion [%]), and Weather Conditions of the Preceding Winter with the Hatching Date of the Tawny Owl *Strix aluco* Clutches (Hatching Date ~ Fixed Effects [Intrinsic Factors, Local Prey, Weather], Random Effects [Territory ID, Year]), Ranking Based on Akaike's Information Criterion (AIC). Also the Values of Effects, Standard Errors (SE), Degrees of Freedom (df), Test Statistics (t) and Probabilities (p) Are Given. In Each Model, the Number of Observations Is 21 and Number of Groups (Years) 8

Fixed effects	Value	SE	df	*t*	*p*	AIC
(Intercept)	126.837	6.960	11	18.224	<0.001	147.623
Male age	2.122	2.459	11	0.863	0.407	
Water voles %	-1.130	0.273	11	-4.135	0.002	
Winter NAO	-2.611	2.255	6	-1.158	0.291	
(Intercept)	121.385	8.274	11	14.670	<0.001	149.322
Male age	2.099	2.529	11	0.830	0.424	
Water voles A	-1.145	0.281	11	-4.080	0.002	
Mean winter temperature	-0.949	1.690	6	-0.562	0.595	
(Intercept)	131.085	8.259	10	15.872	<0.001	149.468
Male age	1.915	2.513	10	0.762	0.464	
Water voles A	-1.706	0.612	10	-2.787	0.019	
Winter NAO	-4.549	2.926	6	-1.555	0.171	
Water voles A:Winter NAO	0.266	0.259	10	1.026	0.329	
(Intercept)	166.219	21.837	10	7.612	<0.001	149.906
Male body mass	-0.120	0.063	10	-1.900	0.087	
Male age	5.301	2.826	10	1.876	0.090	
Water voles A	-0.877	0.291	10	-3.008	0.013	
Winter NAO	-1.914	2.066	6	-0.926	0.390	
(Intercept)	131.770	3.992	12	33.012	<0.001	149.944
Water voles A	-1.001	0.232	12	-4.313	0.001	
Winter NAO	-3.003	2.318	6	-1.296	0.243	
(Intercept)	123.632	6.562	11	18.840	<0.001	150.407
Male age	2.724	2.474	11	1.101	0.295	
Water voles %	-1.219	0.269	11	-4.527	0.001	
(Intercept)	131.281	7.406	11	17.727	<0.001	150.650
Male age	-0.454	2.368	11	-0.192	0.852	
Water voles A	-0.963	0.284	11	-3.395	0.006	
Winter NAO	-4.057	2.607	6	-1.556	0.171	
(Intercept)	120.338	13.778	10	8.734	<0.001	150.749
Male age	3.873	4.816	10	0.804	0.440	
Water voles %	-0.530	2.688	10	-0.197	0.848	
Male age:Water voles %	-0.235	0.898	10	-0.261	0.799	

(Table 6) contd….

Fixed effects	Value	SE	df	*t*	*p*	AIC
(Intercept)	130.232	8.206	9	15.870	<0.001	151.486
Male age	-0.879	2.851	9	-0.308	0.765	
Female age	0.823	2.174	9	0.378	0.714	
Small voles A	0.058	0.349	9	0.168	0.871	
Water voles A	-1.105	0.730	9	-1.513	0.165	
Winter NAO	-3.907	2.726	6	-1.433	0.202	
(Intercept)	135.778	5.244	11	25.894	<0.001	151.663
Water voles %	-1.625	0.601	11	-2.701	0.021	
Winter NAO	-5.007	2.890	6	-1.732	0.134	
Water voles %:Winter NAO	0.281	0.253	11	1.107	0.292	

case the prevalence of water voles, might outweigh the effects of some other variables. Though general regional or larger-scale indices may reveal associations between environmental factors and timing of breeding in owls, the most significant relationships can be found, as expected, as responses to relevant local and intrinsic factors. Present results suggest, that without detailed knowledge on the prey base of the territory, based only on the relatively easily available general small vole abundance indices, misleading results may emerge. The importance of small voles in governing breeding of owls may be overemphasized. However, prey samples from nests concern only the time period of breeding. Before breeding, particularly during winter, the availability of small voles may be of crucial importance for the breeding condition of parent birds and so it may have a decisive indirect effect on timing of breeding.

CONFLICT OF INTEREST

The author confirms that this article content has no conflicts of interest.

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