Diet and reproduction in coastal and inland populations of the Tawny Owl *Strix aluco* in southern Finland

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Abstract

In generalist predators the energy needed for reproduction is derived from various prey categories, the profitability of which may vary according to the biomass or accessibility of the prey items. We examined the relationships between the diet and production of young in two Tawny Owl (*Strix aluco*) populations in southern Finland. We found a positive correlation between the amount of remnants of different prey in samples

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of litter collected from the nest bottoms after breeding and the production of young. Three important prey categories in the diet of owls during the nestling period, i.e. ~~w~~Water ~~v~~Voles, ~~f~~Field ~~v~~Voles and thrush-sized birds, seemed to be significantly related to the number of fledglings. However, only thrush-sized birds showed a significant relationship to the number of fledglings when all prey variables were analysed together in one model. The total prey mass was the best predictor of owl brood size. There were no significant local differences between the effects of different prey categories on the production of Tawny ~~o~~Owl young. Our results, combined with some earlier findings, outline the relationship between food supply and the production of Tawny Owl young in southern Finland. With regards to the Tawny Owl this outline can be generalized to other areas with other kinds of food supply within the distribution range of the species. Similar outlines are probably applicable also to many other generalist predators.

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Zusammenfassung

Nahrung und Reproduktion von Küsten- und Inlandspopulationen des Waldkauzes *Strix aluco* in SüdfinnlandBei generalistischen Beutegreifern setzt sich die für die Reproduktion aufgewendete Energie aus den verschiedenen Beutekategorien zusammen, die je nach Biomasse und Verfügbarkeit der Beutestücke var iie Is this correct? ren können. Wir untersuchten die Beziehung zwischen Nahrung und Jungenproduktion in zwei Waldkauzpopulationen in Südfinnland. Wir fanden eine positive Korrelation zwischen der Anzahl an Beuteresten in Proben aus der Neststreu nach der Brut und der Jungenproduktion der Käuze. Drei bedeutende Beutekategorien in der Nahrung der Käuze während der Nestlingszeit schienen signifikant mit der Anzahl an

Flügglingen zusammenzuhängen: Schermäuse, Erdmäuse und drosselgroße Vögel. Lediglich drosselgroße Vögel zeigten jedoch eine signifikante Beziehung in der Kombination mit allen Beutekategorien. Die gesamte Beutemasse erklärte die Brutgröße der Käuze am besten. Es gab keine signifikanten räumlichen Unterschiede zwischen den Effekten verschiedener Beutekategorien auf die Jungenproduktion der Käuze. In Kombination mit einigen früheren Ergebnissen liefern unsere Resultate einen Grundzusammenhang zwischen Nahrungsbereitstellung und der Produktion von jungen Waldkäuzen in Südfinnland. Innerhalb des Verbreitungsgebietes der Art kann dieser Grundzusammenhang generalisierend auf andere Gegenden mit anderen Arten der Nahrungsbereitstellung angewendet werden. Ähnliche Zusammenhänge sind außerdem vermutlich auch auf viele andere generalistischen Beutegreifer anwendbar.

Keywords

Alternative prey
Arvicola amphibius
Generalist predators
Microtus agrestis
Myodes glareolus
Optimal foraging

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Introduction

A sufficient amount of food is the inevitable prerequisite for every animal activity (e.g. Lack 1954; Newton 1980, 1998; Martin 1987). In the yearly cycle of allocation of resources, reproduction is the main target requiring food in excess over the basic metabolic needs (e.g. Ricklefs 1974; Meijer et al. 1989). In food specialists, the quantity of available food is so decisive that the animals may be forced to skip breeding when their staple food is not available in sufficient amounts (e.g. Newton 1980, 1998; Korpimäki and Hakkarainen 2012).

In comparison, generalists usually have more options because they can shift between various alternative food resources (Lack 1954; Angelstam et al. 1984). The value of these alternatives may, however, vary both quantitatively and qualitatively (MacArthur and Pianka 1966; Krebs et al. 1977; Hakkarainen et al. 1997; Zárybnická et al. 2009). In generalists, the energy needed for reproduction is divided between various prey categories, the profitability of which may vary, for instance, according to the biomass or accessibility of the prey items. Large prey items are, in general, more profitable than small ones, but their profitability may diminish due to difficulties in accessibility or handling. Thus, the most profitable prey items should be abundant, easily accessible and of optimum size for catching and handling (e.g. Newton 1986; Charter et al. 2015; Lourenço et al. 2015).

In various species of birds, the potential upper limit for the production of young is set by the food supply that governs the determination of clutch size before the onset of egg laying (Drent and Daan 1980; Korpimäki and Hakkarainen 1991; Pietiäinen and Kolunen 1993). Food supply and other factors prevailing during the rest of the nesting period determine the final outcome of reproduction. Based on extensive experimentation with the European ~~k~~Kestrel *Falco tinnunculus*, Meijer et al. (1990) suggested that there is a causal chain in the production of young, with food supply determining laying date, which in turn determines clutch size. As in birds of prey in general (Newton 1979), females of the Ural Owl *Strix uralensis* about to lay eggs rely on courtship feeding by males (Lundberg 1980). Thus, it is reasonable to assume that the males of the Tawny Owl *Strix aluco* are nearly always the sole hunter starting from the time the female begins to form eggs up to the time the nestlings are about to leave the nest. Thus, the male is confronted with supplying the female with an adequate food supply consisting of a variety of prey items, which the female converts into reproductive effort.

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In the study reported here we examined how the brood size is fine-tuned by diet during the nestling period in two Tawny Owl populations in southern Finland. The Tawny Owl is a generalist predator, whose diet mainly includes various kinds of small vertebrates (e.g. Southern 1969; Solonen and Karhunen 2002; Balčiauskienė et al. 2005; Kekkonen et al. 2008; Żmihorski et al. 2008). By numbers and by biomass the most important prey of the Tawny Owl are various species of small mammals and birds, with the species composition of they prey varying according to local and temporal availability. Fluctuations and changes in the availability of prey may have marked effects on the diet and breeding of the Tawny Owl (Wendland 1984; Jędrzejewski et al. 1994; Petty 1999; van Veen and Kirk 2000; Baudvin and Jouaire 2003). In Finland, the beginning of the breeding activities in the Tawny Owl seems to be dependent on the availability of small voles (*Microtus* spp., *Myodes* spp.) (Solonen 2013, 2014) or ~~w~~Water ~~v~~Voles *Arvicola amphibius* (Kekkonen et al. 2008; Solonen 2013), while the breeding success (production of young) seems to be governed by the availability of small voles (Solonen and Karhunen 2002).

Our study is based on the assumptions that most of the prey items used by Tawny Owls during breeding are represented in the food remains (including those found in pellets) present on the nest bottom and that samples of these remains represent the proportions that these prey items were brought to the nest. Our aim was to answer three main questions:

1. Is there a single dominant prey category or are there several alternative prey categories that have significant effects on the number of Tawny Owl young produced during the nestling period?
2. Are the numbers of fledglings explained by the numbers or biomass of prey?

3. Are there differences in the relationships between the diet and production of young between coastal and inland populations of Tawny Owls?

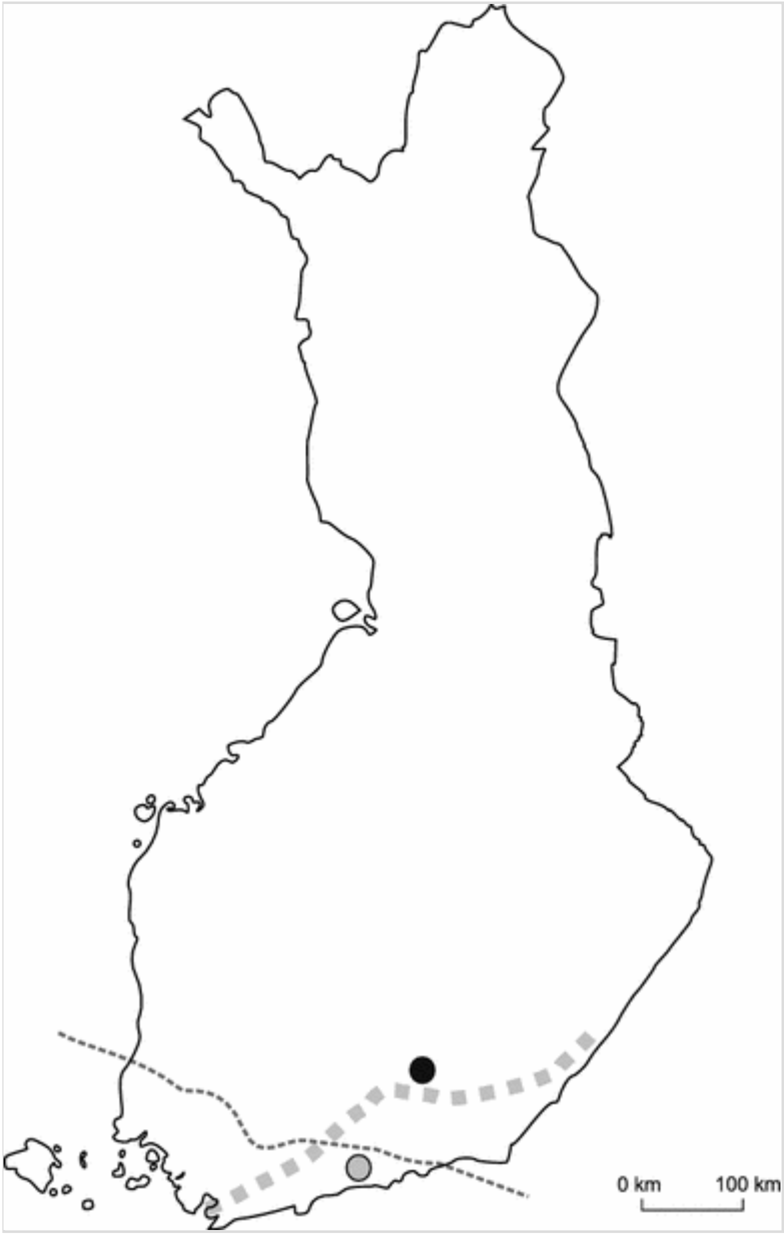
Materials and methods

Study areas

The field work was conducted in two local study areas located approximately 70 km apart (Fig. 1) in different climatic zones (see Hämet-Ahti 1981) between 1989 and 2003. Our coastal study area of about 500 km^2 was situated in Uusimaa, near the southern coast of Finland (60°22′N, 25°15′E), in the hemiboreal climatic zone~~;~~. Our inland study area of about 700 km^2 was located in and around the city of Lahti in Päijät-Häme, southern Finland (60°59′N, 25°39′E), in the boreal climatic zone. The hemiboreal zone halfway between the temperate and boreal zones is characterized by relatively cold winters and mild summers (Hämet-Ahti 1981). The boreal zone is characterized by long, usually very cold winters, and short, cool to mild summers. A prominent characteristic of the inland study area is also the ridge of Salpausselkä, the northern (inland) side of which, in particular, differs in terms of geography and climate from the southern (coastal) lower-lying areas (Kersalo and Pirinen 2009). The study areas consist of a mosaic of agricultural land (approximately 50 %), spruce-dominated forest (40 %) and water systems (10 %), mainly sea bays in the coastal area and lakes and streams in the inland area.

Fig. 1

The location of the study areas in Finland. *Black circle* ~~I~~inland study area, *grey circle* coastal study area, *thin dark-grey dashed line* border of the hemiboreal vegetation zone, *thick light-grey dashed line* terminal moraine formation of Salpausselkä



Owl populations

The general densities of Tawny Owl territories were about six to ten territories per 100 km^2 in the coastal area and three to six territories in the inland area. Large continuous forests were, however, avoided by Tawny Owls. Consequently, the inland area in particular was characterized by a fragmented pattern of Tawny Owl presence. The most suitable areas for Tawny Owls might contain several territories quite nearby each other, while large areas were present that were essentially uninhabitable for this species. The habitats of the owls under study were mainly rural, but some of the territories may be characterized as (sub)urban. The owls preferred rich deciduous and mixed forests near fields, sparsely dispersed human habituation and especially eutrophic water bodies. The preferred Tawny Owl habitats often had a strong cultural impact, being situated around manor houses, which have traditionally occupied the most fertile agricultural land of the area.

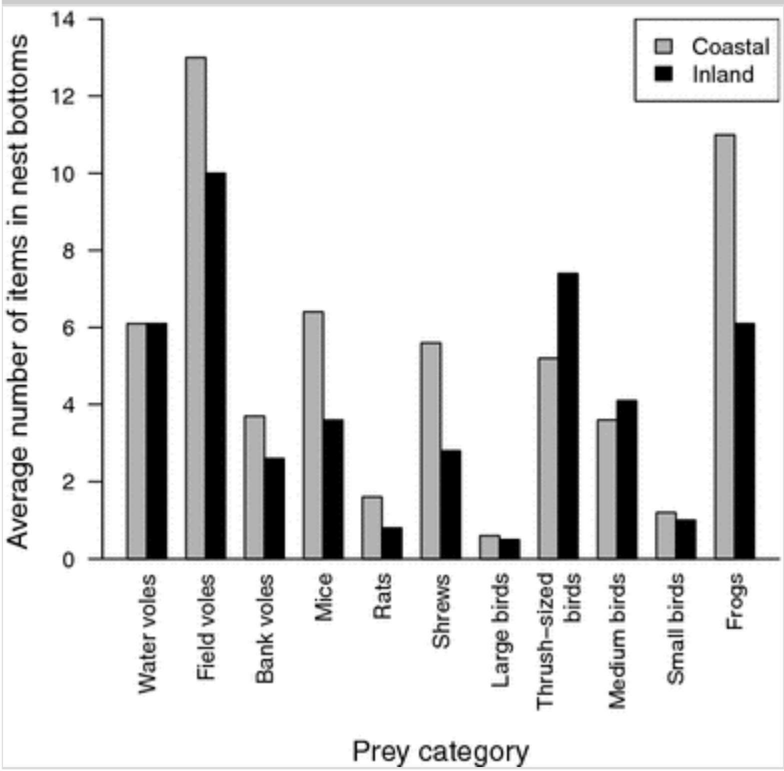
Tawny owl nests found in the nest boxes were visited three to four times during the breeding season to determine clutch size and the number of young fledged. As an estimate of offspring production, we used the number of nearly fledged (about 3–4 weeks old) young in the nest (Solonen 2005). The present data consist of a total of 127 broods, only one of which was unsuccessful.

Prey data

Our total prey data included 5690 prey items sampled from 127 Tawny Owl nests after breeding (Fig. 2). All of the litter on the nest bottom from each nest box sampled was examined. In the coastal study area, the diet of breeding Tawny Owls was studied by analysing 51 samples of nest bottom litter collected from 30 different locations (local territories) between 1986 and 1999 (Solonen and Karhunen 2002). In the inland study area, samples of litter from the bottom of 76 nests from 33 local territories were analysed between 1995 and 2003 (Kekkonen et al. 2008). The total numbers of individual prey items from the two study areas were 2958 and 2732, respectively. We assume here, for simplicity, that prey categories were represented in the food remains (including those found in pellets) of the nest bottom samples in the proportion used during the nestling period of owls. The total number of prey found in the samples are taken to represent minimum values of the actual numbers brought to the nests. Based on our samples, we estimated that an average nestling received at least 825 g food (the average total of 2787 g/brood divided by the average brood size 3.38), which is about twice the mass of a nestling at the time it leaves the nest.

Fig. 2

Average numbers of individuals per nest sample according to different prey categories in coastal and inland populations of the Tawny Owl *Strix aluco* in southern Finland



Food remains (bones) were separated from the litter by picking with tweezers, sorted and identified into the appropriate categories. 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 hip-bones, femurs, tibiae and humeri. Bones were classified as right or left side of the body and paired so that we did not overestimate the number of prey individuals. Species were determined by the unique morphological features of the bones based on both the literature (Saurola 1995; Siivonen and Sulkava 2002) and reference collections. Biomasses were calculated based on the body mass of the species given in the relevant literature (von

Haartman et al. 1963–1972; Korpimäki and Sulkava 1987).

Statistical methods

To examine the importance of different prey categories, we used generalized linear mixed models (GLMM) fit by the maximum likelihood method, using the statistical package "lme4" in R (version 3.2.4; R Development Core Team 2013; Venables et al. 2014). The general formula of the models was as follows:

$$\text{Response variable} \sim \text{Fixed effects} + \text{Random effects, family poisso}$$

The response variable was the number of fledglings produced in a breeding attempt. The fixed effects included a categorical explanatory variable "locality" (coastal, inland), and various food variables. Food variables included the numbers of individuals and the biomass of the most used prey categories found in the nest bottom samples, namely ~~w~~Water ~~v~~Voles, ~~f~~Field ~~v~~Voles *Microtus agrestis*, ~~b~~Bank ~~v~~Voles *Myodes glareolus*, mice, rats, shrews, birds (divided in four size classes) and frogs. The Tawny Owl territory identification, which was used as an indicator of the impacts of the local habitat (and individual birds), and the categorical variable "year", used to indicate other annually varying unknown factors, characterised random effects on the intercepts of the fledgling numbers. Bonferroni correction was used to adjust *p* values due to multiple comparisons.

Results

There was a positive correlation between the amount of remnants of prey in the litter samples collected from the nest bottom after breeding and the number of young produced by the owls (Table 1; Fig. 3). In the total data of prey used during the nestling period, there were three single prey categories, namely ~~w~~Water ~~v~~Voles, ~~f~~Field ~~v~~Voles and thrush-sized birds, which seemed to be significantly ($p < 0.05$) related to the number of fledglings. However, after Bonferroni correction, only the effect of total biomass passed the limit of significance ($p < 0.004$). When all prey variables were put together in one model (Table 2), only thrush-sized birds showed a significant relationship with number of fledglings.

Table 1

Effects of numbers and total biomass of individuals of prey categories in the diet on the fledgling numbers of the Tawny Owl *Strix aluco* in southern Finland based on single generalized linear mixed models

Prey category	Estimate	Standard error	*z*	*p*
Water ~~v~~Voles	0.015	0.006	2.528	0.012
Field ~~v~~Voles	0.008	0.004	2.318	0.020
Thrush-sized birds	0.022	0.010	2.248	0.025
Bank ~~v~~Voles	0.019	0.014	1.371	0.171
Mice	0.008	0.011	0.759	0.448
Medium birds	0.006	0.013	0.442	0.659
Rats	−0.014	0.036	−0.389	0.697
Shrews	0.002	0.009	0.197	0.844
Small birds	−0.005	0.037	−0.121	0.904
Large birds	0.004	0.065	0.062	0.951
Frogs	−0.000	0.000	−0.005	0.996
Total numbers	0.004	0.002	2.378	0.017
Total biomass	0.000	0.000	2.927	0.003

Random effects, indicating spatially and temporally varying unknown factors, were according to territory identification (ID) and year. Degrees of freedom 108

Fig. 3

Relationship between the amount of remnants of prey in samples of the nest bottom litter after breeding and the number of young produced by Tawny

Owls in southern Finland. *Upper panel* ~~N~~number of prey remnants plotted against brood size, *lower panel* total biomass of prey (grams) plotted against brood size

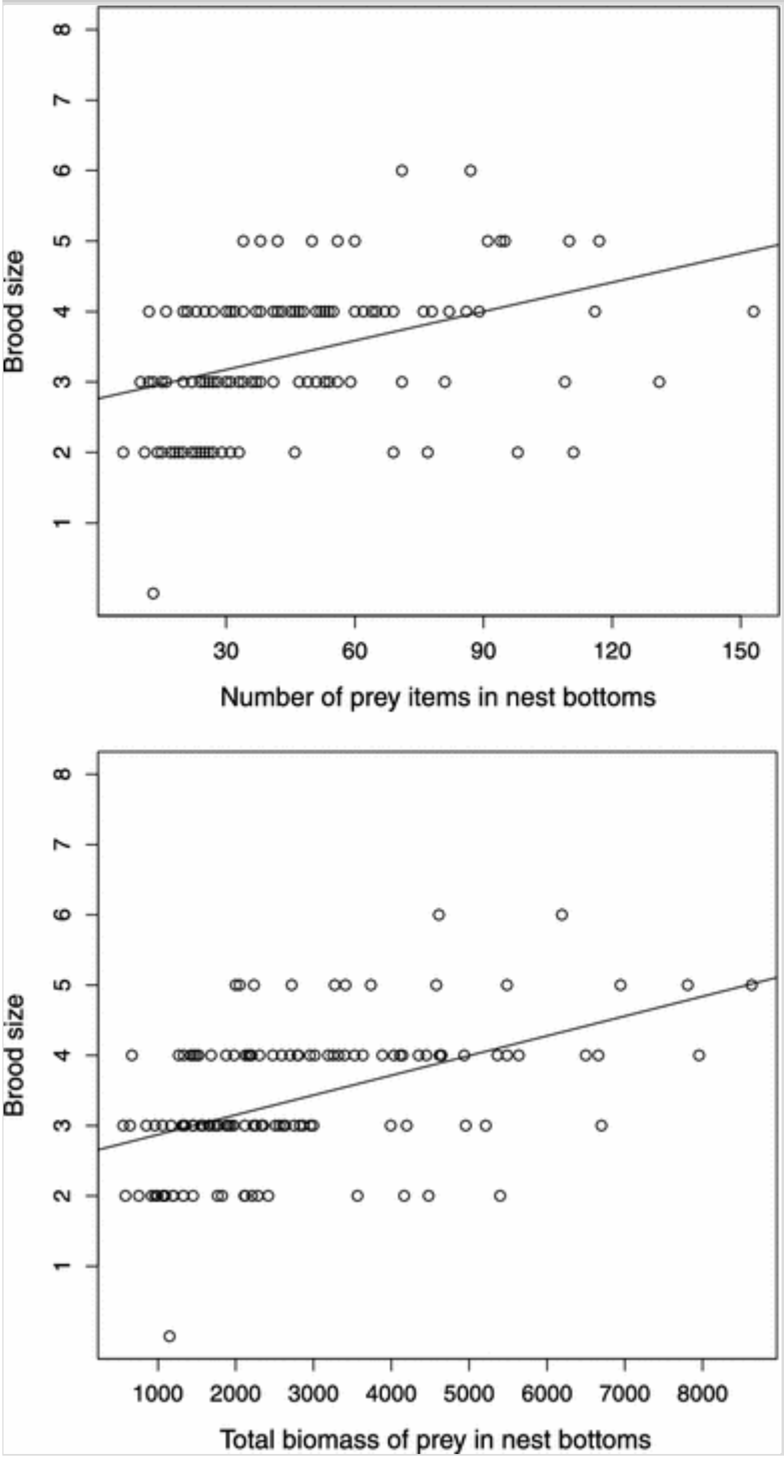


Table 2

Effects of the numbers of individuals and the biomass in the single prey categories in the diet on the fledgling numbers of the Tawny Owl in southern Finland based on generalized linear mixed models of all the variables together

Prey category	**Estimate**	**Standard error**	*z*	*p*
Numbers				
(Intercept)	0.870	0.128	6.814	<0.001
Thrush-sized birds	0.027	0.011	2.508	0.012
Water ~~v~~Voles	0.011	0.008	1.526	0.127
Field ~~v~~Voles	0.007	0.005	1.277	0.202
Mice	0.012	0.014	0.825	0.409
Rats	−0.035	0.049	−0.708	0.479
Medium birds	−0.009	0.016	−0.580	0.562
Frogs	0.004	0.007	0.541	0.588
Large birds	0.020	0.067	0.304	0.761
Bank ~~v~~Voles	−0.005	0.020	−0.249	0.804
Shrews	−0.003	0.012	−0.235	0.814
Small birds	0.002	0.045	0.050	0.960
Biomass				
(Intercept)	0.872	0.127	6.846	<0.001
Thrush-sized birds	0.000	0.000	2.479	0.013
Water ~~v~~Voles	0.000	0.000	1.493	0.135
Field ~~v~~Voles	0.000	0.000	1.272	0.203

Random effects, indicating spatially and temporally varying unknown factors, were territory ID and year. Degrees of freedom 98

~~*SE* standard error~~

Prey category	**Estimate**	**Standard error**	***z***	***p***
Mice	0.001	0.001	0.833	0.405
Rats	−0.000	0.000	−0.707	0.479
Frogs	0.000	0.000	0.583	0.560
Medium birds	−0.000	0.001	−0.577	0.564
Bank vVoles	−0.000	0.001	−0.290	0.772
Large birds	0.000	0.000	0.308	0.758
Shrews	−0.000	0.002	−0.230	0.818
Small birds	0.000	0.004	0.039	0.969

Random effects, indicating spatially and temporally varying unknown factors, were territory ID and year. Degrees of freedom 98

~~*SE* standard error~~

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The available data did not reveal any significant local differences between the effects of different prey categories on the production of Tawny Owl young (Table 3). The brood size of owls (mean ± standard error 3.38 ± 0.09, $n = 127$) differed slightly but not significantly between the coastal (3.22 ± 0.14, $n = 51$) and inland (3.49 ± 0.11, $n = 76$) study areas ($t_{125} = 1.51$, $p = 0.134$).

Table 3

Effects of locality (coastal, inland) and the numbers of individuals in the most important single prey categories in the diet on the fledgling numbers of the Tawny Owl in southern Finland based on generalized linear mixed models

Prey category	**Estimate**	**Standard error**	***z***	***p***
(Intercept)	1.042	0.109	9.528	<0.001

Random effects, indicating spatially and temporally varying unknown factors, were territory ID and year. Degrees of freedom 106

Prey category	**Estimate**	**Standard error**	***z***	***p***
Locality	0.119	0.135	0.881	0.379
Water ~~v~~Voles	0.019	0.011	1.765	0.078
Locality: ~~w~~Water ~~v~~Vole	−0.006	0.013	−0.427	0.669
(Intercept)	1.074	0.105	10.207	<0.001
Locality	0.059	0.133	0.442	0.658
Field ~~v~~Voles	0.007	0.005	1.416	0.157
Locality: ~~f~~Field ~~v~~Vole	0.007	0.008	0.883	0.377
(Intercept)	1.032	0.134	7.727	<0.001
Locality	0.030	0.187	0.163	0.871
Thrush-sized birds	0.025	0.019	1.299	0.194
Locality: birds	−0.005	0.023	−0.212	0.832
(Intercept)	1.056	0.109	9.720	<0.001
Locality	0.158	0.134	1.173	0.241
Bank ~~v~~Voles	0.028	0.018	1.573	0.116
Locality: ~~b~~Bank ~~v~~Vole	−0.009	0.032	−0.288	0.773
(Intercept)	1.069	0.125	8.579	<0.001
Locality	0.130	0.147	0.880	0.379
Mice	0.015	0.014	1.048	0.295
Locality: mice	0.014	0.030	0.451	0.652

Random effects, indicating spatially and temporally varying unknown factors, were territory ID and year. Degrees of freedom 106

On average, Tawny Owl broods received (at a minimum) 2787 ± 1534 (standard deviation) g prey (Table 4). However, there were significant differences between areas (an unbalanced design of the two-factor analysis of variance, $F_{1,84} = 7.13$, $p = 0.009$) and brood sizes ($F_{1,84} = 18.1$, $p < 0.001$). Tawny Owl broods in the coastal area received nearly 600 g more prey than their counterparts inland. Broods with four young received 1100 g more prey than broods with three young. The interaction area × brood size was not significant ($F_{1,84} = 1.21$, $p = 0.274$). The biomass per young in the coastal area was higher than that per young in the inland area ($F_{1,84} = 6.62$, $p = 0.012$), but it did not differ between brood sizes ($F_{1,84} = 2.63$, $p = 0.108$). The interaction area × brood size was not significant ($F_{1,84} = 0.54$, $p = 0.464$).

Table 4

Mean biomasses of prey brought to the nest according to remnants found and the calculated biomass per young in coastal and inland study areas in broods of three and four young of the Tawny Owl

Study area/population	Brood size	Total biomass (g), mean ± SD		Biomass/young (g), mean ± SD		*n*
Coastal	3	2472	1478	824	492	21
	4	4126	1846	1031	461	14
	Total	3134	1807	907	484	35
Inland	3	1988	933	662	311	22
	4	2962	1371	740	342	31
	Total	2557	1293	708	329	53
Total	3	2224	1239	741	413	43
	4	3324	1608	831	402	45
	Total	2787	1534	787	407	88

This was an unbalanced design of two-factor analysis of variance

Data in table are presented as the mean ± standard deviation

Discussion

Our results suggest that thrush-sized birds were the most important prey category affecting the production of Tawny Owl young during the nestling period in our study areas in southern Finland. Earlier results suggested that small voles were of particular importance in the coastal study area (Solonen and Karhunen 2002) while in the inland population, laying date, which was used as a proxy for reproduction, was not related to the abundance of small voles (Kekkonen et al. 2008). Instead, ~~w~~Water ~~v~~Voles had a significant effect on Tawny Owl laying dates. However, only prey weight was used as an explanatory variable in this study. In an earlier study, the extrinsic factors examined also showed no significant relationships to reproduction in the coastal Tawny Owls (Solonen 2009). Discrepancies between the results of these different studies are probably largely due to a number of indirect effects and the inability of the variables used to characterize spatial or temporal conditions with sufficient precision. There are, however, various other factors than diet that additionally affect the outcome of the reproduction made possible by available food resources (Sasvári and Hegyi 2002; Solonen 2009). The food supply before the nestling period and the clutch size that depends on it have a dominant effect on the number of fledglings produced (Solonen 2009). This food supply varies spatially as well as temporally, both annually and during the breeding season of owls. Thus, the owls encounter varying sets of conditions, many of which lead to a similar result in terms of the number of young produced.

As the schedule of temporal variation in the availability of food is essential for the growth and survival of nestlings, any change, such as that caused by a changing climate, will cause problems for birds (e.g. Naef-Daenzer and Keller 1999). In the Ural Owl, the underlying vole cycle defines yearly breeding success (Brommer et al. 2002); any change in the environment may cause changes in vole dynamics (Brommer et al. 2009) and, consequently, in owl breeding success. In the Common Buzzard, warming early spring temperatures seem to have advanced breeding of the Finnish population (Lehikoinen et al. 2009). However, because early summer temperatures have remained the same, advanced breeding schedule may have forced the young to hatch in a less favourable environment than previously.

The optimal foraging theory predicts that when faced with two prey types, predators should maximize consumption of high-quality and easy-to-capture prey, increasing nutritional value while reducing energetic costs of capture, thus maximizing intake rates (MacArthur and Pianka 1966; Krebs et al. 1977). If two species of prey of equal nutritional value and equal capture costs are available, the factor determining the choice of prey will likely be the relative density of the two prey types. The alternative prey hypothesis suggests that the functional and numerical response of predators to fluctuating rodent populations results in cyclic variation in predation pressure on other available prey, such as birds (Lack 1954; Angelstam et al. 1984). During recent decades, annual fluctuations in small vole populations have also declined, at least in some coastal areas in southern Finland (Solonen and Ahola 2010). This has coincided with a decrease in the number of breeding Tawny Owl~~ population~~s (T. Solonen, personal data), which suggests that there is some causal relationship between the decline in the vole populations and that in owl populations. Unfortunately, population fluctuations and trends of the ~~w~~Water ~~v~~Vole have not been monitored as well as those of the smaller vole species. However, it would appear that during the nestling period, the availability of birds and ~~w~~Water ~~v~~Voles to the Tawny Owl populations in our study largely dampened the effects of population fluctuations of small voles on the production of young, which supports the alternative prey hypothesis.

Elsewhere in Europe, the average production of Tawny Owl young seems to be lower than that reported in our study, varying locally by about twofold at around two and three fledglings (Wendland 1984; Ranazzi et al. 2000; Baudvin and Jouaire 2003; Roulin et al. 2003; Marchesi et al. 2006). Small rodents are, in general, the most important prey category during breeding (Southern 1969; Jędrzejewski et al. 1994; Petty 1999; Balčiauskienė et al. 2005), but in some cases birds may be of primary importance (Kirk 1992; Marchesi et al. 2006). Compensatory temporal changes in the importance of different prey categories in the diet of Tawny Owls due to long-term trends in the prey populations have also been observed (Wendland 1984; Petty 1999).

According to the individual optimization hypothesis (Perrins and Moss 1975), in each brood the prey biomass per young should be more or less similar regardless of brood size. This was exactly what we observed: nestlings in broods with three and four young received similar amounts of food. However, in both brood size classes coastal young received more food, possibly reflecting general differences in average productivity between the two areas. Accordingly, the numbers of voles were higher in the rich and low-lying habitats of the coastal areas than in the less fertile areas inland. However, bird prey were more abundant inland.

Conclusions

Our results, combined with some earlier findings, provide an outline of the relationship between food supply and production of Tawny Owl young in southern Finland. This outline suggests that the availability of small voles, in particular ~~f~~Field ~~v~~Voles, determines the clutch size of the Tawny Owl (Solonen et al. 2015) which, in turn, sets the upper limit to the number of young. The abiotic environmental conditions and timing of breeding broadly determine what kinds of prey are best available during the nesting period (Sonerud 1986; Nybo and Sonerud 1990). Based on general observations, the early breeders of late winter and early spring depend on overwintered, still declining populations of small voles—at least until the snow melts. Later in spring, ~~w~~Water ~~v~~Voles and increasing numbers of migratory birds as well as nestlings and fledglings, in particular thrush-sized birds, become an essential resource (T. Solonen et al., unpublished results). This outline can be generalized to other areas with other kinds of food supply within the distribution range of the Tawny Owl. Similar outlines are probably also applicable to many other predators, where the production of young depends on various kinds of alternative prey which may fluctuate and vary annually and during the breeding season.

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Compliance with ethical standards

The authors declare that they have no conflict of interest. All applicable institutional and/or national guidelines for the care and use of animals were followed.

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