The difference between generalist and specialist: the effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators

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Abstract

Specialist individuals within animal populations have shown to be more efficient foragers and/or to have higher reproductive success than generalist individuals, but interspecific reproductive consequences of the degree of diet specialisation in vertebrate predators have remained unstudied. Eurasian pygmy owls (hereafter POs) have less vole-specialised diets than Tengmalm's owls (TOs), both of which mainly subsist on temporally fluctuating food resources (voles). To test whether the specialist TO is more limited by the main prey abundance than the generalist PO, we studied breeding densities and reproductive traits of co-existing POs and TOs in central-western Finland during 2002-2019. Breeding densities of POs increased with augmenting densities of voles in the previous autumn, whereas breeding densities of TOs increased with higher vole densities in both the previous autumn and the current spring. In years of vole scarcity, PO females started egg-laying earlier than TOs, whereas in years of vole abundance TO females laid eggs substantially earlier than PO females. The yearly mean clutch size and number of fledglings produced of both POs and TOs increased with abundance of voles in the current spring. POs laid large clutches and produced large broods in years of both high and low vole abundance, whereas TOs were able to do so only in years of high vole abundance. POs were able to raise on average 73% of the eggs to fledglings whereas TOs only 44%. The generalist foraging strategy of POs including flexible switching from main prey to alternative prey (small birds) appeared to be more productive than the strictly vole-specialized foraging strategy of TOs. In contrast to earlier studies at the individual-level, specialist predators at the species level (in this case TOs) appear to be less effective than generalists (POs), but diet specialisation was particularly costly under conditions when scarcity of main foods limited offspring production.

Keywords: Boreal forest, , foraging, predator-prey interactions, pygmy owl, reproductive success, specialist-generalist continuum, Tengmalm's owl, vole cycle.

Introduction

Fluctuations in food availability are probably one of the main factors modifying variation in life-history traits linked to reproduction among individuals, ultimately regulating population dynamics (Lack 1954). The importance of food limitation for population dynamics and reproduction can be evaluated by studying effects of food supply availability on breeding densities and reproductive success, or by experimental manipulations (addition or reduction) of food supply. Among vertebrates, birds have been the most frequent subject of food-supplementation experiments during the reproductive season (Boutin 1990, Ruffino et al. 2014). A vast majority of food-manipulation experiments showed that supplemented birds usually advanced the initiation of egg-laying, produced larger clutches and attained larger reproductive success relative to non-supplemented birds (Martin 1987, Ruffino et al. 2014), which shows food limitation on breeding performance. However, there are only a handful of studies that have experimentally provided food during winter, before the breeding season, to study the food limitation on breeding densities of birds, and a vast majority of these studies have been conducted with one clade, the tits (*Paridae*) (Newton 1998). The reason probably is that it is difficult and laborious to conduct experiments, in which food supply of bigger birds with large home ranges would be experimentally manipulated in late winter and early spring.

Lack (1954) postulated that “to prove that numbers of a bird are effectively limited by its food supply, the observer must not only measure the abundance and availability of its chief foods and the quantity of each consumed, but must ……. study interaction between the numbers of the bird and those of its prey over a period of years”. Fortunately, there are many birds, such as seed-eaters, bird-eaters and rodent-eaters, which subsist on pulsed food resources showing large temporal fluctuations in abundance. Therefore, “nature” manipulates their main food resources, and thus the interactions between numbers of birds and their foods have been most often studied with these birds, showing that the breeding densities of these birds fluctuate in close accordance with their main foods (see e.g. Reinikainen 1937, reviews in Newton 1980, 1998).

Limitation of main foods on breeding densities and reproductive success of specialist predators is expected to be larger than on that of generalist predators (e.g. Newton 1980). This is because specialists use a narrow spectrum of food resources while generalists use a wider range of resources, although in fact there is a continuum from specialization to generalization both within- and between-species (Partridge and Green 1985, Korpimäki 1986, Rechner 1990, Korpimäki and Krebs 1996, Durell 2000). Diet specialisation may be associated with the spatio-temporal heterogeneity and predictability in the abundance of food resources, cultural experience, and the evolution of efficient foraging adaptations (Whitfield 1990). Anatomical, morphological, behavioural and physiological adaptations should give greater foraging efficiency for specialists than generalists (Sherry 1990). Therefore, specialists utilizing a narrow range of foods are predicted to be more efficient in utilizing their main food than generalists using a larger variety of foods (MacArthur and Pianka 1966, review in Stephens and Krebs 1986). Several studies in vertebrates have evaluated the relative efficiency of specialist-generalist strategies between different individuals in the same population. Specialist individuals were often shown to be more efficient foragers and/or to have higher reproductive success than generalist individuals (review in Terraube et al. 2011, but see Whitfield et al. 2009, Navarro-López et al. 2014). However, there could also be a trade-off associated with specialisation, as specialists could be less efficient than generalists in subsisting on alternative foods, when the main food is scarce (Rechner

1990, Huckins 1997). Until recently, this issue has received inadequate research attention, particularly in terrestrial predators (but see Terraube et al. 2011), despite its important implications for the persistence and conservation of populations of specialist predators. In particular, interspecific reproductive consequences of the degree of diet specialisation in vertebrate predators have remained unstudied so far, although specialist species are expected to be at greater risk of extinction than generalist species (e.g. Ferrer and Negro 2004, Shultz et al. 2005).

Birds of prey are widespread study objects for food limitation on population densities, breeding performance and reproductive success because the abundance and availability of their main foods can be relatively accurately estimated in the field. Therefore, firm evidence for food limitation on population densities and life-history traits of birds of prey subsisting on pulsed food resources (e.g. small rodents, lagomorphs and game birds) have been demonstrated by several research groups in boreal and arctic regions (e.g. Adamcik et al. 1978, Newton and Marquiss 1986, Korpimäki 1987a, Korpimäki and Hakkarainen 1991, Korpimäki and Norrdahl 1991, Rohner 1996, Nielsen 1999, Salamolard et al. 2000, Tornberg et al. 2005, Therrien et al. 2014). However, to our best knowledge, there are no long-term studies analysing food limitation on population dynamics, breeding performance and reproductive success of coexisting predators with different degrees of diet specialisation under temporally fluctuating conditions of the main foods in the same area, thus excluding other confounding temporal or spatial factors.

We investigate the effects of food limitation on breeding densities and reproductive success of two small owl species with varying degree of diet specialisation: the Eurasian pygmy owl (*Glaucidium passerinum*; hereafter pygmy owl) and Tengmalm’s owl (*Aegolius funereus*). Pygmy owl is the smallest owl species in Europe (Mikkola 1983).

For both species the main prey are small mammals (Kellomäki 1977, Korpimäki 1988). In Northern Europe, pygmy owls are however considered more generalist predators than the Tengmalm’s owl and larger owls such as the long-eared owl (*Asio otus*), the short-eared owl (*A. flammeus*) and the hawk owl (*Surnia ulula*) (reviewed in Korpimäki 1992), because at least during spring they are often able to shift to alternative prey, particularly to small birds during periods of main food scarcity (Kellomäki 1977). This is supported by the fact that the proportion of small birds in the diet of pygmy owls in spring was 45% of prey number (Kellomäki 1977), whereas for Tengmalm’s owls the corresponding figure was only 10% (Korpimäki 1988) in two nearby areas in central-western Finland. In addition, the diet width of pygmy owls in the breeding season was larger than that of Tengmalm’s owls (Korpimäki and Hakkarainen 2012). However, the main foods of both pygmy and Tengmalm’s owls were bank voles (*Myodes glareolus*) and *Microtus* voles (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*) in central-western Finland (Korpimäki and Hakkarainen 2012). We conducted in our study area (central-western Finland) a contemporary comparison of the annual variation in breeding densities and reproductive traits of pygmy and Tengmalm's owls in relation to fluctuations of their main food resources (bank and *Microtus* voles). A high-amplitude three-year population cycle has been prevailing in the study area (central-western Finland) since late 1970s (Korpimäki et al. 2005, Korpela et al. 2013), which sets the scene for examining how these two predators with different degrees of specialisation respond to the variation in their main prey. Because pygmy owls have less specialised diets than Tengmalm’s owls at least during the breeding season, we predict that (i) pygmy owls are better able to shift to alternative prey, and thus the among-year variation in their breeding density estimates is smaller than in Tengmalm’s owls. We further expect that limitation of main foods is less important in the initiation of egg-laying of pygmy owls than of Tengmalm's owls whereas more vole-specialised latter species is more efficient than former species in taking benefits from years of vole abundance. This predicts that (ii) egg-laying of pygmy owls starts earlier than that of Tengmalm's owls in years of vole scarcity, whereas Tengmalm's owls initiate egg-laying earlier in years of vole abundance. In addition, (iii) less vole-specialised pygmy owls lay large clutches and produce more fledglings than do more-specialised Tengmalm's owls in years of both low and high abundance of main foods, whereas Tengmalm's owls are able to produce large clutches and broods only in years of vole abundance, and have overall more variation in their reproductive traits that is explained by variation in main food abundance.

Material and methods

Study area

The study was conducted in the same area where long-term studies on Tengmalm's owl population have been conducted: the Kauhava region, central-western Finland (63º N, 23º E) covering approximately 1000 km^2 (Korpimäki 1987a, Korpimäki and Hakkarainen 1991, 2012). The landscape consisted of commercially managed pine- and spruce-dominated forests with some birch-dominated patches, interspersed with clear-cut areas, agricultural land and peatland bogs (Hakkarainen et al. 2003). The proportion of old-growth forest in our study area was low as a consequence of continuous forestry practices (i.e. clear-cutting and thinning; Hakkarainen et al. 2003). Nest-boxes for Tengmalm's owls were provided from 1966 onwards (up to 2019), and for pygmy owls during 2002-2019. The diameter of the entrance hole of Tengmalm's owl boxes was 80 to 100 mm, and that of pygmy owl boxes was 45 mm.

The nest-box project for pygmy owls was initiated in 56 forest patches in autumn 2001. From 2004 onwards the number of forest patches was 150 and reached a maximum of

285 patches in 2015 (mean and range no. of patches 212 and 56-285 per year during 2002-19). In each forest patch (hereafter called as box-site), two nest-boxes for pygmy owls were provided during 2002-2019. Two boxes were placed per site 80-100 m apart because Siberian flying squirrels (*Pteromys volans*) also often use these nest-boxes for roosting and reproduction throughout the year (Turkia et al. 2018), and this ensured availability of the nest-site and food-storing site for pygmy owls (Masoero et al. 2018). Approximately 80 natural cavities, excavated by great-spotted woodpeckers (*Dendrocopos major*), were inspected annually during the study period, but only two nests were found in them. The two owl species do not compete for available cavities and nest-boxes; pygmy owls do not breed in cavities with large entrance-holes and Tengmalm's owls cannot enter the cavities used by pygmy owls (Korpimäki and Hakkarainen 2012, Morosinotto et al. 2017). The yearly total number of Tengmalm's owl nest-boxes ranged from 450 to 470 during 2002-2019, and these nest-boxes and known natural cavities (approx. 30-40) made by black woodpeckers (*Dryocopus martius*), were inspected each spring (Korpimäki 1987a, Korpimäki and Hakkarainen 1991, 2012).

The two owl populations in our study area were not constrained by the availability of nesting sites, because even in good vole years characterized by highest owl densities , only 33% of Tengmalm's owl boxes during 1973-2009 (Korpimäki and Hakkarainen 2012) and 31% of pygmy owl box-sites during 2002-2019 (this study) were occupied. Nest boxes were also relatively evenly distributed across the landscape: average distance between available pygmy owl nest-box sites was 1.4 km and between available Tengmalm's owl boxes 0.8 km. The pooled density of pygmy owl nest-boxes and natural cavities suitable for pygmy owls was similar to that of natural cavities in primeval coniferous forests of southern Finland (Pakkala et al. 2018a, 2018b). The density of Tengmalm's owl nest-boxes in our study area (approximately 1 nest-box per 2 km^2) does not substantially differ from natural conditions: the density of suitable natural cavities in pristine coniferous forests of southern Finland is 0.5-1.5 per km^2 (Virkkala et al. 1994). In addition, in coniferous forests managed for forestry in Central Sweden, the density of natural cavities made by black woodpeckers, the size of which also is suitable for Tengmalm's owls, is 0.3-0.4 per km^2 (Johnsson et al. 1993).

Population and reproductive data

All owl boxes, and known natural cavities, were inspected twice every spring (in April and again in late May to early June) to detect breeding attempts. In a majority nests of both owl species, clutch size, hatching date, and number of hatchlings and fledglings were recorded, as well as fledglings were ringed, and a majority of the parent owls were ringed and/or re-captured (see Korpimäki and Hakkarainen 1991, 2012, Morosinotto et al. 2017).

Vole abundance data

Abundances of voles have been estimated by snap-trappings each year in mid-May and in late September in the western and middle part of the study area. Both in the western and middle part, four plots were sampled both in May and September (i.e. cultivated field, abandoned field, spruce forest, pine forest; see Korpimäki et al. 2005 for more details on trapping methods and vole cycles). Fifty to 60 Finnish metal mouse snap traps were set at 10 m intervals in vole runways in each plot and were checked once a day for three days. Thus, the area of a sample plot ranged from 0.5 to 0.6 ha. The results from 3-night trapping periods were pooled and standardized to the pooled number of bank and *Microtus* voles caught per 100 trap nights (later called as density estimate of voles in the current spring and in the previous autumn).

Statistical analyses

We analysed the difference in the main breeding characteristics between the two owl species while taking into account the abundance of the main prey. The following response variables for the breeding characteristics of both species were used: annual number of occupied nests per 100 nest-boxes, yearly mean and standard deviation (SD) of the laying date, yearly mean clutch size and yearly mean number of fledglings produced per breeding attempt. The number of nests per 100 boxes was log-transformed to obtain more normal distribution. For each of the five response variables we tested the null model and four linear models (LMs) combining the explanatory variables: species (pygmy owl or Tengmalm's owl) and the density estimate of voles (pooled number of *Microtus* and bank voles trapped per 100 trap nights) either in the current spring or the autumn preceding the breeding season. The number of cases (years) was 18 in each model. Interactions between the two variables (species and one of the vole density estimates) were also tested. The five resulting models (null model and models with or without the interaction and with the two different density estimate of voles) were ranked in order of AICc values (Akaike Information Criterion corrected for small sample size). To consider top models we used a difference in terms of AICc (ΔAIC) lower than 2, but for an easier representation only the top model is shown. The final model was validated using the plots of residuals versus the fitted values. Model selection tables are reported in the Supplementary material. LMs were run using R v 3.6.1 (R Core Team 2019).

To further analyse whether density estimates of voles in the current spring or previous autumn better explained reproductive variables of pygmy and Tengmalm's owls, linear regressions were used for the annual data from 2002-2019. Log-transformed number of nests per 100 boxes, mean laying date, mean clutch size, mean number of hatchlings and mean number of fledglings per breeding attempt in two owl species were regressed against density estimates of voles. Long-term trends in numbers and parameters of reproduction during 2002-2019 were analysed with Pearson correlations. Regression analyses and Pearson correlations were performed with IBM SPSS Statistics 23.

Results

The proportion of nest-sites occupied by pygmy owls varied from 1 nest to 31 nests per 100 box-sites during 2002-2019 (Table 1, Fig. 1, upper panel). The corresponding variation in the proportion of nest-boxes occupied by Tengmalm’s owls ranged from 1 to 27 nests per 100 boxes inspected during 2002-2019. The model including owl species and pooled density estimate of *Microtus* and bank voles (later vole density index) in the previous autumn (but no interaction) best explained the among-year variation in the breeding density estimate of both pygmy and Tengmalm’s owls (Table 2, Supplementary material, Table S1). In species-specific regression analyses, the breeding density of pygmy owls was explained by the density index of voles in the previous autumn but not by that in the current spring (Fig. 1, lower panel, Table 3).The breeding density of Tengmalm’s owls was better explained by the density estimate of voles in the previous autumn, but also the regression coefficient for vole indices in the current spring was significant (Fig. 1, lower panel, Table 3). The breeding density of pygmy owls significantly declined in the course of the 18-year study period (Fig. 1, upper panel, r = -0.65, p = 0.003, n = 18) whereas the declining trend for Tengmalm’s owls was not significant (r = -0.21, p = 0.41, n = 18).

The yearly mean laying date of the pygmy owl population varied from 4 April to 23 April with a mean of 12 April during 2002-2019 (Fig. 2, Table 1). Pygmy owls started egg-laying on average 4 days later than Tengmalm’s owls (Fig. 2, Table 1). The variation in the mean laying date of the two owl species was best explained with a model including the density index of voles in the previous autumn and its interaction with owl species (Table 2, Fig. 3, upper panel). Tengmalm's owl females initiated egg-laying already one-two weeks earlier than pygmy owls in good vole years but in poor vole years one-two weeks later than pygmy owls (Fig. 2). The yearly mean laying date of pygmy owls varied clearly less than that of Tengmalm's owls (coefficient of variation 47.2% vs. 142.2%, respectively). The standard deviation of the laying dates of the Tengmalm's owl population increased with augmenting densities of voles in the current spring, but no such trend was evident for the standard deviation of laying dates of the pygmy owl population (Fig. 3, lower panel, Table 2). In species-specific regression analyses, the mean laying date of pygmy owls was not closely related to the vole abundance indices of the current spring or previous autumn (Fig. 3, upper panel, Table 2), whereas laying dates of Tengmalm's owls became earlier with increasing densities of voles in both the previous autumn and the current spring (Fig. 3, upper panel, Table 2). There was no significant long-term trend in the yearly mean laying date of the pygmy owl ($r = 0.30$, $p = 0.23$, $n = 18$) or the Tengmalm's owl ($r = 0.06$, $p = 0.82$, $n = 18$) population.

The yearly mean clutch size of the pygmy owl population varied from 5.8 to 8.3 eggs with a mean of 7.0 eggs during 2002-2019, whereas the range of the yearly mean clutch sizes of Tengmalm's owls was from 4.4 to 6.6 eggs with a mean of 5.4 eggs per clutch (Fig. 4, upper panel, Table 1). In all the 18 years, the mean clutch size of pygmy owls was markedly larger than that of Tengmalm's owls. The model including owl species and vole density index in the current spring (but no interaction) best explained the among-year variation in mean clutch sizes of the two owl species; thus both species had larger clutch sizes with higher vole density in the current spring (Fig. 4, lower panel, Table 2). Species-specific regression analyses revealed that the mean clutch size of either owl species was not correlated with vole density in the previous autumn but was closely correlated with vole density in the current spring (Table 3). There were no obvious long-term trends in the yearly mean clutch sizes of either pygmy or Tengmalm's owl populations (r = 0.20, p = 0.33, n = 18 and r = -0.06, p = 0.81, n = 18, respectively).

The yearly mean number of hatchlings of the pygmy owl population averaged 6.1 chicks per brood with 87.0% of the eggs hatching during 2002-2019 (Table 1). The corresponding figures were 4.3 chicks and 80% for Tengmalm's owls. Species-specific regression analyses revealed that the number of hatchlings of both owl species increased with augmenting abundances of voles in the current spring (Table 3). There was a significant decreasing long-term trend in the yearly mean number of hatchlings of the pygmy owl population during the 18-year study period (r = -0.51, p = 0.03, n = 18), whereas no trend was found for Tengmalm's owls (r = -0.31, p = 0.29, n = 18).

The yearly mean number of fledglings of the pygmy owl population averaged 5.1 owlets per brood (Table 1, Fig. 5). while that of Tengmalm's owls was 2.4 fledglings. Pygmy owls were thus able to raise 73% of the eggs laid to fledglings whereas the corresponding proportion was only 44% for Tengmalm's owls. All in all, pygmy owls produced 54% more fledglings per nesting attempt than Tengmalm's owls during the 18-year period. The model best explaining among-year variation in the number of fledglings produced per clutch in pygmy and Tengmalm's owls included owl species and vole density index in the current spring but there was no interaction (Table 2). In species-specific regression analyses, there were close positive relationships of yearly numbers of fledglings produced by both owl species with the vole density indices in the current spring but not in the previous autumn (Table 3, Fig. 5).

There was a nearly significant decreasing long-term trend in the yearly mean number of fledglings produced by pygmy owls during the study period (r = -0.46, p = 0.05, n =

18), whereas the corresponding decreasing trend was significant for Tengmalm's owls (r = -0.60, p = 0.008, n = 18).

Discussion

A unique advancement of this study was that we were able to investigate Lack's (1954) postulation on limitation of main foods on the breeding densities and breeding performance of two forest-dwelling predator species with less and more vole-specialised diets in the same study area and the same long-term study period. In our study system, the availability of main foods and habitats was the same for both species, facilitated solid analyses of the differences in population dynamics and life-history traits of two predator species that differ in the degree of food specialisation.

We found that breeding densities of pygmy owls increased with augmenting densities of voles in the previous autumn, whereas in Tengmalm's owls, breeding densities were closely correlated with vole densities in both the previous autumn and the current spring. In late autumn and early winter, pygmy owls collect large food stores in natural cavities and nest-boxes for over-winter survival (Halonen et al. 2007, Terraube et al. 2017, Masoero et al. 2018), whereas Tengmalm's owls are not able to do so probably because larger cavities suitable for them are also accessible to larger food robbers, such as pine martens (*Martens martens*) (Korpimäki and Hakkarainen 2012). The proportion of forest-sites with a food-store of pygmy owls increased with the vole abundance in the current autumn (Masoero et al. 2018), and also numbers of over-wintering adult (+1-year old) female pygmy owls and hatch-yearlings of both sexes increased with vole abundance in the current autumn (Masoero et al. 2020). This resulted in higher breeding densities in the next spring. Consistently with our prediction (i), among-year variation in the breeding density estimates was substantially smaller in pygmy than in Tengmalm's owls. Because pygmy owls have less vole-specialised diets, they are better able to shift to alternative prey in years of vole scarcity. Therefore, pulsed food resources (three-year high-amplitude population cycle of voles) limited the breeding densities of pygmy owls to a smaller extent than that of Tengmalm's owls and relatively more pygmy owls bred in our study area in low vole years. Large food-stores of pygmy owls during late autumn to early winter (Terraube et al. 2017, Masoero et al. 2018, 2020) likely contribute to the body condition of female owls in early spring so that they can lay eggs in approximately same time independently of abundance of main food resources prior to and during the egg-laying period. Tengmalm's owls are not able to collect large food stores for over-winter survival and are thus more dependent on every-day food intake. When main food resources are abundant, female Tengmalm's owls can put on weight (Korpimäki 1990) and start egg-laying very early (in March) but when main food resources are scarce, they have to collect body reserves for longer time and are able to lay eggs only one to one-and-half month later. Both pygmy and Tengmalm's owls are so small that they cannot accumulate large internal fat reserves and are thus more income breeders than capital-breeding larger owls (e.g. Brommer et al. 2004).

In both species egg-laying initiated earlier in higher vole abundance, but as predicted (ii), pygmy owls started egg-laying earlier than Tengmalm's owls in years of vole scarcity, whereas Tengmalm's owl females initiated to lay eggs substantially earlier than pygmy owl females in years of vole abundance. Therefore, there was markedly less variation in the mean laying date of the pygmy owl population than in that of the co-existing Tengmalm's owl population. This showed that limitation of main foods is less important in the initiation of egg-laying of less vole-specialised pygmy owls than in that of more vole-specialised Tengmalm's owls which in turn appeared to be more efficient than former species in taking benefits from years of vole abundance. This interpretation is also supported by the fact that the variation (standard deviation) of the laying dates of Tengmalm's owls increased with the vole abundance in the current spring, while no such relationship was observed in pygmy owls. When voles were abundant, both resident and new late-incoming Tengmalm's owl females were able to put on weight and start to lay eggs rapidly, which induced large intra-year variation in laying dates. Tengmalm's owl males are resident on their territories after first breeding attempt (Korpimäki 1987b), whereas females show long-distance natal and breeding dispersal (Korpimäki et al. 1987, Korpimäki and Lagerström 1988). Therefore, females find mates only gradually, which induces wide variation in laying dates in years of main food abundance. In addition, some early-laying females desert their broods when nestlings are half-grown, re-mate and breed again in the same breeding season when voles are abundant (Korpimäki et al. 2011). Some 10-20% of male Tengmalm´s owls in good years breed with a second or even third female on average two weeks after the first female has started egg-laying (Korpimäki 1991), whereas only one polygynous male has been recorded in our pygmy owl population (E. Korpimäki unpublished data). Polyandry and polygyny induce several late egg-laying initiations in the Tengmalm's owl population and increase standard deviation of the yearly mean laying dates in years of vole abundance. Yearly laying dates of pygmy owls averaged only four days later than those of Tengmalm's owls.

Consistently with our prediction (iii), less vole-specialised pygmy owls laid large clutches and produced more fledglings than more-specialised Tengmalm's owls in years of both scarcity and abundance of main foods, whereas Tengmalm's owls were able to produce large clutches and broods only in years of vole abundance. This might be induced by the fact that smaller species should have faster life-styles and produce on average more eggs and offspring than larger ones. Nation-wide ringing data in Finland showed that brood sizes of pygmy owls at the age of ringing (3-4 weeks) were one to two owlets larger than those of Tengmalm’s owls (Lehikoinen et al. 2011), but these data were pooled from both low and high abundance years of main foods. Pygmy owl females usually start their incubation from the second last egg (Schönn 1980) resulting in that the hatching span (time between first- and last-hatched chicks) average only three days (Siivonen 2013), whereas Tengmalm’s owl females initiate incubation from the second egg (Korpimäki 1981) resulting in much longer hatching spans (average 7 days; Valkama et al. 2002). Our results showed that pygmy owls are usually able to raise all hatchings until the fledging phase, because chick mortality during the nestling period was very low even in years of vole scarcity. This “all-or-none” strategy is facilitated by the more generalized diets of pygmy owls: they are able to shift to alternative prey, particularly to small birds and their nestlings and fledglings in years of scarcity of main foods (Kellomäki 1977). In contrast, long hatching spans ensuing large size hierarchy in Tengmalm’s owl broods facilitate brood reduction during the nestling period in years of vole scarcity, which results in high mortality of small(est) chicks during the nestling period (Valkama et al. 2002). Therefore, vole-specialised Tengmalm’s owls were able to raise large broods only in years of main food abundance. We showed that pygmy owls raised 73% of the eggs laid to fledglings whereas the corresponding proportion was only 44% for Tengmalm’s owls during 2002-2019. The low productivity of Tengmalm’s owls was mainly induced by starvation of owlets during the nestling period, because there was no marked interspecific difference in the proportion of hatched eggs. In addition, the proportion of predated nests was low in both owl species in our study area (<5% of breeding attempts; Korpimäki and Hakkarainen 2012). All in all, pygmy owls produced 54% more fledglings than Tengmalm’s owls during the 18-year period. Pygmy owls have flexible hunting mode, in which they can switch from low-perch sit-and-wait strategy when hunting small mammals to high-perch strategy with only short perching times when hunting birds (Kullberg 1995). Tengmalm's owls in turn mainly use low-perch sit-and-wait hunting mode (Korpimäki and Hakkarainen 2012).

We conclude that the more generalized foraging strategy of pygmy owls, which were flexibly able to shift from main prey (voles) to alternative prey (small birds), was more successful in reproduction than the vole-specialized foraging strategy of Tengmalm's owls under the largely fluctuating food conditions of boreal forests. Therefore, specialist predators (in this case Tengmalm's owls) may be less effective in reproduction than generalist ones (pygmy owls) even when their main foods are abundant, because even at years of high main food abundance mortality in Tengmalm's owl nests was relatively high. Diet specialisation was however particularly costly under conditions, in which scarcity of main foods limited offspring production. Our results from this interspecific comparison contradict a majority of the results of earlier studies conducted at the individual level within species, in which specialist individuals were often shown to have higher reproductive success than generalist individuals (review in Terraube et al. 2011). For example, in two harrier species mostly subsisting on voles, and birds and reptiles serving as alternative prey, the more specialised species (the pallid harrier *Circus macrourus*) attained better hunting success and higher food intake in a year of vole abundance than the sympatric, less specialised species (the Montagu's harrier *C. pygargus*), whereas in years of low vole abundance, the latter species had higher hunting success and food intake (Terraube et al. 2011). However, reproductive consequences for the harriers remained unstudied.

Our results from two owl species with different degree of diet specialization indicated that a generalist strategy may generally be more efficient and productive in terms of offspring production. The following results from Eurasian kestrels (*Falco tinnunculus*) and golden eagles (*Aquila chrysaetos*) were consistent with this suggestion at the intra-specific level. Individual kestrels adopting more generalist strategy in their diet choice were able to produce offspring with better body condition and immuno-competence, and thus have larger fitness potential (Navarro-López et al. 2014). In golden eagles, generalist pairs appeared to obtain higher reproductive success than specialist ones (Whitfield et al. 2009). Predators specialising on main food supply are probably pressed to occupy habitat patches with an abundance of this resource, or to consume much time and energy in searching for main foods over large areas (Begon et al. 2005, Santangeli et al. 2012). If future studies confirm that specialist predators are less effective than generalists when their main foods are scarce, then diet specialisation may be really costly when human-induced habitat degradation reduces, for example, patches of old-growth forests with rich food supply in boreal regions. This would help to explain, why specialist species are usually more vulnerable and at greater risk of extinction than generalist species (e.g. Ferrer and Negro 2004, Shultz et al. 2005).

Data Availability Statement

The data are available from DRYAD upon acceptance of the paper for publication

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Authors' contributions

EK and TL conceived the ideas and designed methodology; EK, KH and GM collected the data; EK, GM and TL analysed the data; EK and TL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material

Table S1. Model selection table. The number of nests was log-transformed to obtain more normal distribution. In the models the two explanatory variables are included without (+) or with (*) interaction between them. Voles.spr= vole density index in the current spring and voles.prev.au= vole density index in the autumn preceding the breeding season.

Response	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Nests per 100 boxes (log)	species + voles.prev.au	4	0.17	8.96	0.000	0.617
	species * voles.prev.au	5	1.04	9.92	0.959	0.382
	species * voles.spr	5	-5.04	22.09	13.132	0.001
	species + voles.spr	4	-6.72	22.73	13.773	0.001
	(Null model)	2	-9.91	24.18	15.222	0.000
Mean laying date	species * voles.prev.au	5	-122.49	256.99	0.000	0.564
	species + voles.prev.au	4	-124.26	257.82	0.830	0.373
	species + voles.spr	4	-126.84	262.97	5.984	0.028
	(Null model)	2	-129.56	263.48	6.490	0.022
	species * voles.spr	5	-126.27	264.54	7.551	0.013
S.D. laying date	species * voles.spr	5	-100.55	213.10	0.000	0.875
	species + voles.spr	4	-104.08	217.45	4.354	0.099
	species + voles.prev.au	4	-105.70	220.69	7.588	0.020
	species * voles.prev.au	5	-105.64	223.28	10.183	0.005
	(Null model)	2	-112.82	230.01	16.911	0.000
Mean clutch size	species + voles.spr	4	-25.52	60.32	0.000	0.795
	species * voles.spr	5	-25.52	63.03	2.709	0.205
	species + voles.prev.au	4	-35.38	80.04	19.721	0.000
	species * voles.prev.au	5	-34.75	81.49	21.167	0.000
	(Null model)	2	-52.80	109.97	49.645	0.000

Mean no. of fledglings	species + voles.spr	4	-45.19	99.67	0.000	0.778
	species * voles.spr	5	-45.10	102.20	2.528	0.220
	species + voles.prev.au	4	-51.49	112.28	12.604	0.001
	species * voles.prev.au	5	-50.82	113.64	13.967	0.001
	(Null model)	2	-70.24	144.85	45.179	0.000

Figure Legends

Fig. 1. Upper panel: The number of nests of pygmy owls per 100 sites with two nest-boxes inspected (solid line and dots) and the number of nests of Tengmalm’s owls per 100 nest-boxes inspected (dashed line and triangles) during 2002-2019.

Lower panel: The log-transformed number of nests of pygmy and Tengmalm’s owls against the density index of voles (the pooled number of *Microtus* voles, the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*, and bank voles *Myodes glareolus* trapped per 100 trap-nights) the previous autumn during 2002-2019.

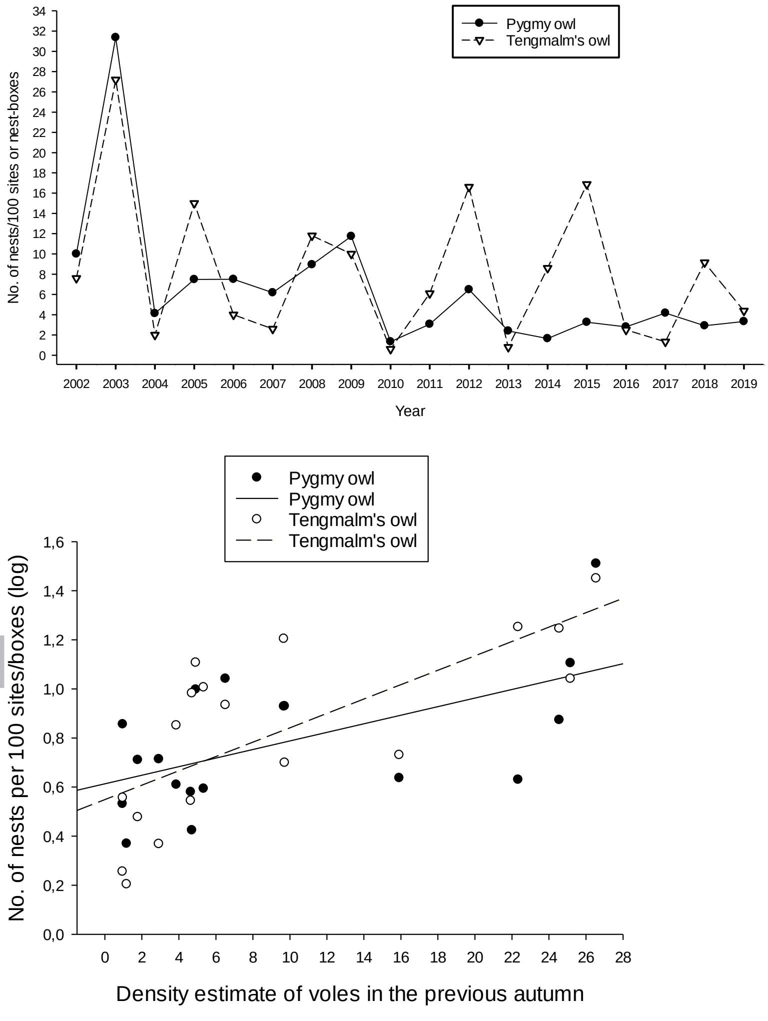

Fig 2. Yearly mean laying date (±S.D., 1= 1 Apr, 2= 2 Apr, etc.) of pygmy owls (dots and solid line) and Tengmalm's owls (triangles and dashed line) during 2002-2019.

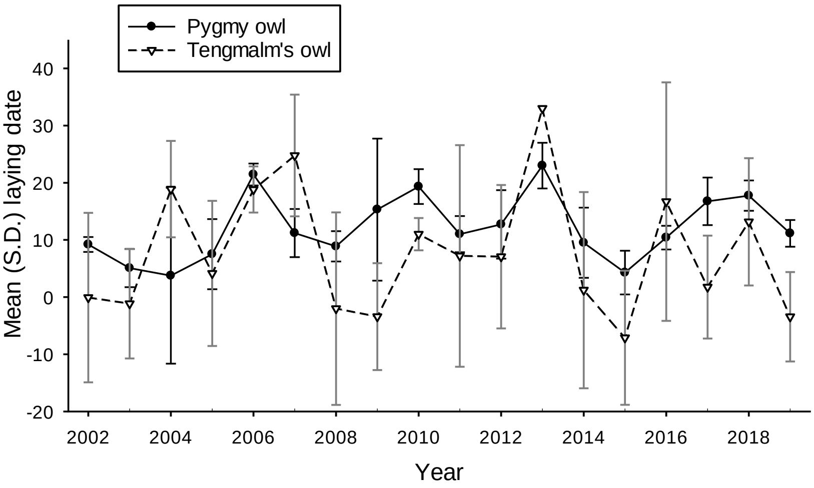

Fig. 3. Upper panel: The yearly mean laying date (1 = 1 Apr, 2 = 2 Apr, etc.) of pygmy owls (dots and solid line) and Tengmalm’s owls (circles and dashed line) against the density estimates of voles (the pooled number of *Microtus* and bank voles trapped per 100 trap-nights) in the previous autumn during 2002-2019.

Lower panel: The yearly standard error of mean laying date of pygmy owls (dots and solid line) and Tengmalm’s owls (circles and dashed line) against the density estimates of voles (the pooled number of *Microtus* and bank voles trapped per 100 trap-nights) in the current spring during 2002-2019. Linear regression r= 0.14, p= 0.60 for pygmy owls and r= 0.59, p=0.009 for Tengmalm’s owls.

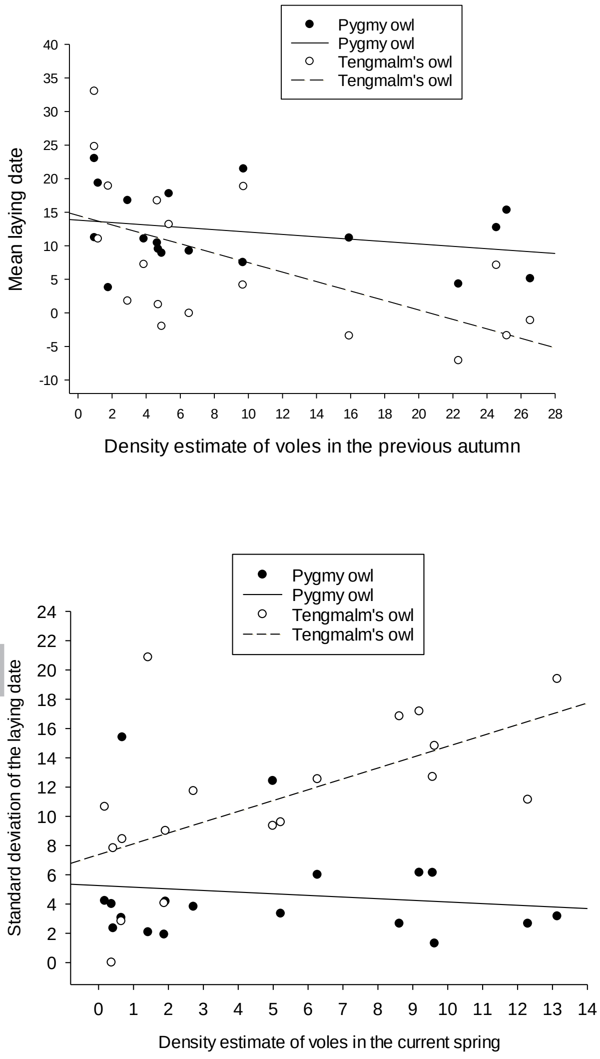

Fig. 4. Upper panel: The yearly mean clutch size (±S.D) of pygmy owls (dots and solid line) and Tengmalm's owls (triangles and dashed line) during 2002-2019.

Lower panel: The yearly mean clutch size of pygmy owls (dots and solid line) and Tengmalm's owls (circles and dashed line) against the density estimates of voles (the pooled number of *Microtus* and bank voles trapped per 100 trap-nights) in the current spring during 2002-2019.

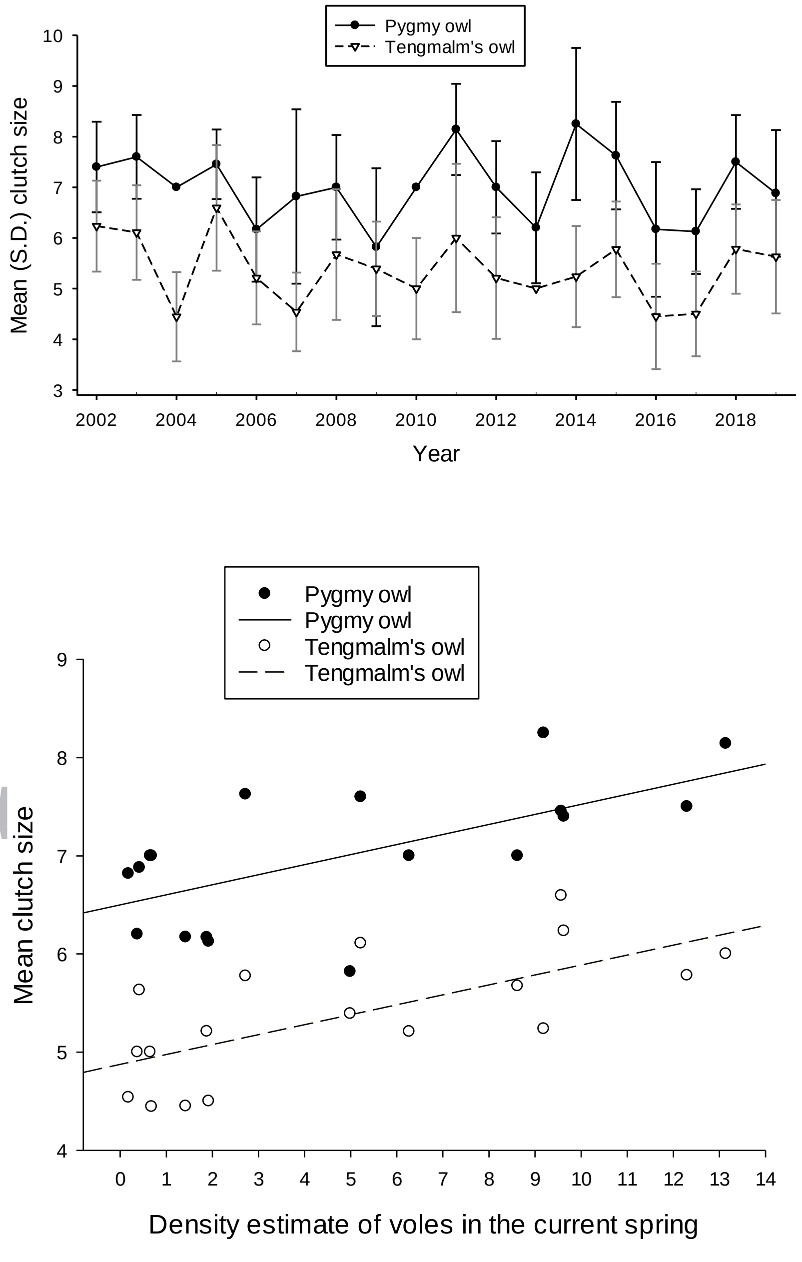

Fig. 5. The yearly mean number of fledglings (±S.D) of pygmy owls (dots and solid line, black S.D.) and Tengmalm's owls (circles and dashed line, grey S.D.) against the density estimates of voles (the pooled number of *Microtus* and bank voles trapped per 100 trap-nights) in the current spring during 2002-2019.

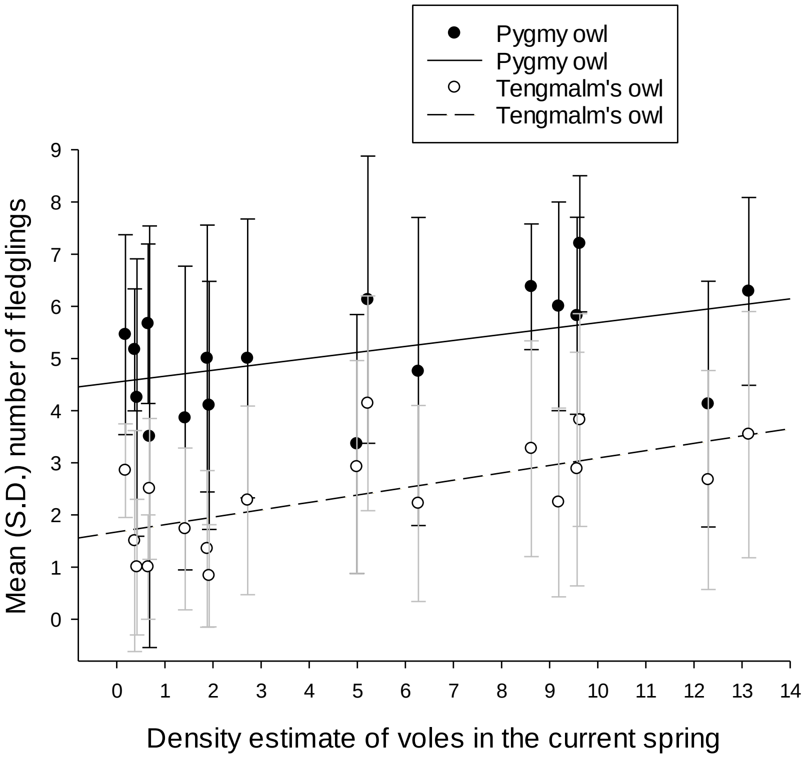

Table Legends

Table 1. Population and reproductive parameters of pygmy and Tengmalm's owl in the study area during 2002-2019. Number of study years (N), no. of nests per 100 box-sites or boxes, as well as annual minimum, maximum, mean and standard deviation of laying date, clutch size, no. hatched and no. fledged owlets are given.

	N	Minimum	Maximum	Mean	S.D.
Pygmy owl					
No. of nests	18	1.3	31.4	6.6	6.9
Laying date	18	3.8	23.0	12.1	5.7
Clutch size	18	5.8	8.3	7.0	0.7
No. hatched	18	4.0	7.8	6.1	1.1
No. fledged	18	3.4	7.2	5.1	1.1
Tengmalm's owl					
No. of nests	18	0.6	27.2	8.2	7.2
Laying date	18	-7.1	33.0	7.8	11.1
Clutch size	18	4.4	6.6	5.4	0.7
No. hatched	18	2.2	5.7	4.3	1.0
No. fledged	18	0.8	4.1	2.4	1.0

Table 2. Summary of the best linear models (LMs) explaining the breeding density estimates, mean and standard deviation of the laying dates, mean clutch sizes and mean numbers of fledglings of pygmy and Tengmalm's owls during 2002-2019. The number of nests per 100 sites/boxes was log-transformed which resulted in more normal distribution. The symbol "*" denotes the interaction between the two variables; in these models also both main effects were included. Voles.spr = vole density index in the current spring and voles.prev.au = vole density index in the previous autumn. Significant variables ($P < 0.05$) are shown in bold. For the categorical variable "owl species" parameter estimates are given relative to the reference category "Tengmalm's owl".

Response	Explanatory	Estimate ± SE	Dfs	F	P
Nests per 100 box-sites (log)	(Intercept)	0.557 ± 0.075			
	owl species	0.048 ± 0.084	1,33	0.33	0.568
	voles.prev.au	0.023 ± 0.005	1,33	24.42	**<0.0001**
Mean laying date	(Intercept)	13.816 ± 2.671			
	owl species	0.715 ± 3.777	1,32	2.82	0.103
	owl species * voles.prev.au	-0.528 ± 0.290	1,32	3.31	0.078
	voles.prev.au	-0.177 ± 0.205	1,32	9.25	**0.005**
S.D. laying date	(Intercept)	5.266 ± 1.505			
	owl species	2.110 ± 2.128	1,32	20.58	**0.0001**
	owl species * voles.spr	0.853 ± 0.324	1,32	6.94	**0.013**

	voles.spr	-0.112 ± 0.229	1,32	3.77	0.061
Mean clutch size	(Intercept)	6.504 ± 0.156			
	species (TO vs. PO)	-1.632 ± 0.171	1,33	90.94	**<0.0001**
	voles.spr	0.102 ± 0.020	1,33	26.32	**<0.0001**
Mean no. of fledglings	(Intercept)	4.479 ± 0.269			
	owl species	-2.738 ± 0.296	1,33	85.81	**<0.0001**
	voles.spr	0.128 ± 0.034	1,33	13.92	**0.0007**

Table 3. Linear regression estimates (r ± S.E.) of log-transformed number of nests, mean laying date, mean clutch size and number of fledglings per breeding attempts in pygmy and Tengmalm's owls against vole density estimates of voles (pooled number of *Microtus* and bank voles trapped per 100 trap nights) in the current spring and previous autumn during 2002-2019.

	Pygmy owl				Tengmalm's owl			
	Voles spring		Voles autumn		Voles spring		Voles autumn	
	r	p	r	p	r	p	r	p
Log(no. of nests)	0.14±0.29	0.57	0.57±0.24	0.01	0.60±0.31	0.01	0.73±0.26	0.001
Laying date	1.19±5.78	0.45	0.28±5.65	0.26	0.37±10.64	0.13	0.58±9.33	0.01
Clutch size	0.64±0.55	0.004	0.01±0.73	0.96	0.69±0.48	0.01	0.39±0.62	0.11
No. hatched	0.47±1.01	0.047	-0.14±1.13	0.57	0.67±0.80	0.003	0.43±0.96	0.07
No. fledged	0.46±1.00	0.05	0.14±1.11	0.58	0.64±0.79	0.05	0.25±0.99	0.33