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Authors: Liang, Hongchun, Li, Ning, and Chen, Zhaorong

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The prey tactics by two owl species in the forest of northeastern China

Hongchun LIANG, Ning LI and Zhaorong CHEN*

Department of Plant Protection, Tianjin Agricultural University, 22 Jinjinglu, Xiqing, Tianjin 300384, China; e-mail: lianghongchun@tjau.edu.cn

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Abstract. The Japanese scops owl (*Otus semitorques*) and Ural owl (*Strix uralensis*), found in the forests of northeastern China, differ in body size and foraging tactics, and are thus expected to prey on different rodent species. We hypothesized that the Japanese scops owl, an active predator, would prey on smaller and younger individuals than the Ural owl, a sit-and-wait predator. We used pellet analyses to evaluate selection of rodents by the two owls in relation to prey species, age, and size. Although the two owl species consumed a wide range of food items, rodents constituted the most common prey with the greatest biomass in the Japanese scops owl. The Japanese scops owl also foraged on insects and birds, whereas the Ural owl complemented its diet of rodents with spiders, scorpions and snakes. The Japanese scops owl selected smaller and younger rodents and the Ural owl preyed on larger and older individuals. Morphology and behaviour of both prey and predators may explain this differential predation between the two species.

Key words: Japanese scops owl, Ural owl, rodent, foraging, prey selection

Introduction

Predation is a significant factor influencing prey population dynamics (Ives & Dobson 1987, Copp & Kováč 2003, Barraquand et al. 2015), not only because of the numbers of individuals taken by predators, but also the abundance of prey species (Robertshaw & Harden 1986, Eubanks & Denno 2000) or specific size or age of prey (Marti & Hogue 1979, Quinney & Ankney 1985, Manderson et al. 2000, Mejlgaard et al. 2013). Some studies have shown that selective predation based on sex or conspicuous characteristics may alter prey sex ratios or social structure (Karanth & Sunquist 1995, Brousseau et al. 2001, Sonerud et al. 2013). Morphological and behavioural variation in both prey and predators may explain selective predation (Molles & Pietruszka 1983, Einfalt & Wahl 1997, Green & Côté 2014). In addition, foraging tactics, handling time and risk of injury as well as sensory capabilities of prey and predator can have significant effects on prey selection (Jaksić & Marti 1981, Kotler 1985, Greene 1986, Trejo 2006) and the susceptibility of prey, defined as the proportion of encounters resulting in prey capture, tends to be negatively correlated with prey size and age (Greene 1986). Juveniles and subadults are more vulnerable because they are often non-territorial, inexperienced, and have yet to fine-tune their sensory capabilities (Brown & Twigg 1971, Morse 1980, Trejo 2006).

A predator's diet within a mixed assemblage of prey is also influenced by the predator's foraging tactics (Greene 1986). The Japanese scops owl (*Otus semitorques*) generally seeks prey while flying (actively searching) although they occasionally make use of perches (Verzhutskii & Ramanujam 2002). In contrast, the Ural owl (*Strix uralensis*) relies on a strategy of ground-foraging and the frequent use of perches, suggesting that this owl is predominantly a sit-and-wait predator (Lundberg 1981, Suzuki et al. 2013). Although both owls use vision to hunt, the Japanese scops owl is capable of seeing at lower light intensity than the Ural owl (Marti 1974).

The primary goal of this study was to evaluate the diet of two owl species relative to selection of rodents by species, size, and age. According to De Arruda Bueno & Motta-Junior (2008), a general feature of predator-prey interactions is that ambush (sit-and-wait) predators often take larger and older prey, relative to those taken by active predators. Thus, we hypothesized that, for rodent species common in the diet of both owls, the Ural owl would consume larger and older prey than the Japanese scops owl.

* *Corresponding Author*

Material and Methods

Predator species

The Japanese scops owl *Otus semitorques* is widely distributed throughout the forest of China, whereas the Ural owl is only distributed in the forest of northeastern China. Both owls build nests in the cavities of high trees, produce one or two broods per year and feed mainly on rodents year-round (Norberg 1987, Pietiainen 1989, Suzuki et al. 2013).

Study area

The study was conducted in natural reserves of TianJin, northeastern China (117°41′ S, 40°05′ W). The environment is defined by a warm temperate, semi-humid and continental monsoon climate, with mild, dry winters, hot summers, and distinct wet (June-September) and dry (October-May) seasons.

Pellets collection and analysis

Owl pellets were collected monthly at nest and roosting sites of the Japanese scops owl and the Ural owl from August 2013 to July 2015. Based on behavioural observations of individual roosting and nest sites, it was determined that these pellets were produced by seven individual Japanese scops owls and five Ural owls. Mandibles, teeth, and crania were separated and used to identify prey species based on a reference collection from the study area. The number of individuals consumed was estimated by first pairing mandibles and then counting unpaired mandibles as additional specimens. Skulls from pellets were not a good estimator because they were frequently broken and sometimes missing. To estimate the body mass of rodents found in the diet, we used measurements of mandible length and body mass of specimens previously collected from the study site (Hamilton 1980, Dickman et al. 1991).

Prey age and size analysis

We used linear regression to elucidate the relationship between body mass and mandible length (Longland & Jenkins 1987, Copp & Kováč 2003) following log-transformation of variables prior to analysis (Hamilton 1980). All regressions were significant ($P < 0.01$, Table 1). We defined age classes by tooth-wear analysis when teeth were available. However, as teeth were not always present in the mandibles, this analysis was not always possible. We associated tooth-wear pattern of some previously collected specimens to their body mass to establish this relationship. We calculated the mean body mass of individuals found in the pellets and grouped them accordingly. This analysis was conducted for the four prey species: the China forest mouse (*Apodemus draco*; juveniles: 5.9-14.61 g, subadults: 14.62-19.86 g, adults: > 19.87 g), the striped field mouse (*A. agrarius*; juveniles: 4.0-12.32 g, subadults: 12.33-18.40 g, adults: > 18.41 g), the brown rat (*Rattus norvegicus*; juveniles: 8.87-19.61 g, subadults: 19.62-34.17 g, adults: > 34.18 g), and the Siberian chipmunk (*Tamias sibiricus*; juveniles: 15.42-28.72 g, subadults: 28.73-45.27 g, adults: > 45.28 g).

Sample rodents collection

Eight lines of pitfall traps were installed to determine rodent abundance. A line consisted of two parts with four buckets (100 l) on each; pitfalls distributed 10 m apart were placed along a plastic drift-fence (35 m long and 0.6 m high). Pitfall lines were separated by 100 m. The 16 lines (a total of 64 pifalls) were opened three days per month and checked every day, resulting in 4608 trap-nights. Pitfall sampling was conducted during the same period as pellet collection. All captured rodents were identified, sexed, weighed, ear-tagged, and released. Only first captures of each individual per month were considered in our analyses. Pitfall traps are considered more effective at capturing higher species numbers, less common species, and younger individuals than some other trapping methods (Pelikán et al. 1977, Hice & Schmidly 2002, Umetsu et al. 2006, Caceres et al. 2011).

Experimental protocol and data analysis

We compared the abundance of species and age classes of rodents in the diet to those captured by trappings, as in Thomas & Taylor (1990) and Plumpton & Lutz (1994), using Bonferroni confidence intervals. A one-way repeated measure analysis of variance (ANOVA), was used to compare prey size in the pellets and in

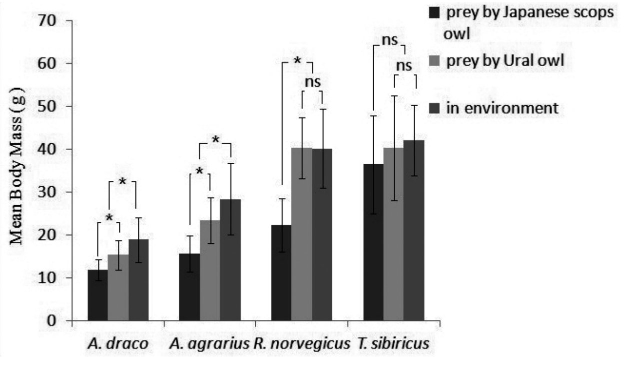

Fig. 1. Comparative analysis of rodent size selection by the Japanese scops owl and the Ural owl. Date are mean ± SE. *: P < 0.05; ns: P > 0.05.

the free range (Zar 1984). For all analyses, statistical significance was set at $p < 0.05$. To avoid comparing samples of distinctly different size, we did not use the complete data set for all comparisons. To compare mean mass of prey consumed by two owls with that found in trappings, we calculated the mean mass from a randomly selected subset. For our study, we defined an opportunistic predator as one that consumed all prey species relative to their abundance in the environment. Conversely, a selective predator was defined as one that consumed disproportionately more of a prey species relative to their occurrence (Jaksić 1989, Lesinski et al. 2008).

Table 1. Regression equations and coefficients of determination (r^2) for relationships between the mandible length and body mass of small mammal species found in the diet of both owls. Values of *P* < 0.01 were for all equations.

Prey species (N)	Equation	r^2
Apodemus draco (72)	Log Y = 5.37(log X) – 3.47	0.71
Apodemus agrarius (36)	Log Y = 5.72(log X) – 2.31	0.83
Rattus norvegicus (28)	Log Y = 6.07(log X) – 5.27	0.76
Tamias sibiricus (24)	Log Y = 6.87(log X) – 5.93	0.92

Table 2. Bonferroni confidence interval analysis to evaluate rodent species selection. [a]If the expected usage (availability; *Pio*) was greater than the upper confidence interval estimate, the prey species was consumed less than expected (–). A *Pio* lower than the lower confidence interval estimate suggests that the prey species was consumed more than expected (+). If an expected proportion fell within the confidence interval, prey were consumed in proportion to their availability (=).

Prey species	Observed prey frequency (*Pi*)		Trapping frequency (*Pio*)	Bonferroni confidence interval for *Pi*		Selectiona [a]	
	Japanes scops owl	Ural owl		Japanese scops owl	Ural owl	Japanese scops owl	Ural owl
Apodemus draco	0.821	0.734	0.727	0.794 ≤ Pi ≤ 0.832	0.743 ≤ *Pi* ≤ 0.831	+	+
*Apodemus agrari*us	0.112	0.035	0.237	0.094 ≤ *Pi* ≤ 0.125	0.031 ≤ *Pi* ≤ 0.065	–	–
Rattus norvegicus	0.145	0.113	0.139	0.131 ≤ *Pi* ≤ 0.148	0.102 ≤ *Pi* ≤ 0.139	=	=
Tamias sibiricus	0.062	0.163	0.058	0.058 ≤ *Pi* ≤ 0.071	0.153 ≤ *Pi* ≤ 0.191	=	+

Results

Rodents availability

The rodent community of the nature reserves of TianJin comprised four potential prey species for both owls. *Apodemus draco* made up 46.6 % (252/541) of all individuals trapped, followed by *A. agrarius* (29.6 %, 160/541), *Rattus norvegicus* (14.8 %, 80/541) and *Tamias sibiricus* (9.1 %, 49/541).

Japanese scops owl diet

We collected 736 Japanese scops owl pellets (mean 31.2 ± 14.8 pellets per month) and 41 samples of pellet debris (fragmented pellets collected during different months and at different sites). Rodents made up 61.3 % of all individuals consumed (N = 3361 individuals) and 83.9 % of total biomass ingested. Mean number of rodent individuals per pellet was 2.8 ± 1.3 (mean ± SD); rodents were found in 90 % of pellets. Insects comprised 31.5 % of all prey items, but only 2.9 % of total biomass. Mean number of insects individuals per pellet was 5.2 ± 3.3, and insects were found in 35 % of the pellets. Birds and amphibians (4.3 % of total prey items and 8.5 % of total biomass) were also represented in the diet. Among rodents (N = 2060 individuals), *Apodemus draco* (71.4 %) was the most frequently recorded prey item throughout the two years, followed by *Rattus norvegicus* (12.9 %), *A. agrarius* (10.5 %) and *Tamias sibiricus* (5.2 %). Japanese scops owls consumed *Apodemus draco* more than expected, *Tamias sibiricus* and *Rattus norvegicus* in proportion to their availability, whereas *A. agrarius* was consumed less than expected (Table 2).

Ural owl diet

The diet of Ural owls was based on analysis of 256 pellets (mean pellet number per month: 24.1 ± 11.8) and 16 samples of pellet debris, yielding 1024 individual rodents. The mean number of rodents found per pellet was 3.2 ± 1.8 (mean ± SD). Rodents were the most abundant food item, representing 50.2 % of 2040 individuals consumed and 68.5 % of the total biomass consumed. Other prey items included small amphibians and snakes (together 15.4 % of the total items and 28.4 % of the biomass ingested) and other invertebrates such as spiders and scorpions (a combined 34.4 % of the prey items and 3.1 % of ingested biomass). Among rodents (N = 1024 individuals), *Apodemus draco* (67 %) was the most frequently recorded prey item throughout the two years, followed by *Tamias sibiricus* (17.5 %), *Rattus norvegicus* (11.4 %) and *A. agrarius*

Table 3. Bonferroni confidence interval analysis to evaluate age selection of preyed rodents. Selection symbols as defined in Table 2.

Prey species age classes	Observed prey frequency (*Pi*)		Trapping frequency (*Pio*)	Bonferroni confidence interval for *Pi*		Selection	
	Japanese scops owl	Ural owl		Japanese scops owl	Ural owl	Japanese scops owl	Ural owl
Apodemus draco							
Juvenile	0.548	0.443	0.453	$0.492 \leq Pi \leq 0.532$	$0.392 \leq Pi \leq 0.511$	+	=
Subadult	0.283	0.392	0.214	$0.281 \leq Pi \leq 0.419$	$0.369 \leq Pi \leq 0.419$	+	=
Adult	0.094	0.164	0.413	$0.083 \leq Pi \leq 0.109$	$0.153 \leq Pi \leq 0.189$	–	+
Apodemus agrarius							
Juvenile	0.613	0.321	0.512	$0.602 \leq Pi \leq 0.683$	$0.292 \leq Pi \leq 0.359$	+	=
Subadult	0.314	0.214	0.278	$0.301 \leq Pi \leq 0.347$	$0.201 \leq Pi \leq 0.292$	+	–
Adult	0.034	0.331	0.043	$0.031 \leq Pi \leq 0.042$	$0.291 \leq Pi \leq 0.342$	–	+
Rattus norvegicus							
Juvenile	0.523	0.217	0.510	$0.508 \leq Pi \leq 0.521$	$0.208 \leq Pi \leq 0.284$	+	–
Subadult	0.245	0.485	0.274	$0.211 \leq Pi \leq 0.286$	$0.410 \leq Pi \leq 0.506$	=	=
Adult	0.180	0.312	0.194	$0.173 \leq Pi \leq 0.192$	$0.213 \leq Pi \leq 0.314$	–	=
Tamias sibiricus							
Juvenile	0.456	0.216	0.410	$0.397 \leq Pi \leq 0.484$	$0.179 \leq Pi \leq 0.289$	=	–
Subadult	0.467	0.327	0.482	$0.417 \leq Pi \leq 0.514$	$0.318 \leq Pi \leq 0.410$	=	=
Adult	0.071	0.383	0.124	$0.057 \leq Pi \leq 0.112$	$0.287 \leq Pi \leq 0.392$	–	=

(4.1 %). Ural owls consumed *Apodemus draco* and *Tamias sibiricus* more than expected, *A. agrarius* less than expected, and *Rattus norvegicus* in proportion to their availability (Table 2).

Prey size and age classes

Smaller individuals of *Apodemus draco* and *Apodemus agrarius* were consumed by Japanese scops owls more than by Ural owls (d.f. = 1, $F_1 = 16.38$, $P_1 < 0.05$; d.f. = 1, $F_2 = 19.14$, $P_2 < 0.05$), but both owls had no size selection for *Tamias sibiricus* (d.f. = 1, F = 4.23, $P > 0.05$) (Fig. 1). Japanese scops owls preyed on smaller individuals of *Rattus norvegicus* (d.f. = 1, F = 18.47, $P < 0.05$), whereas Ural owls had no size selection for this species (d.f. = 1, F = 0.23, $P > 0.05$) (Fig. 1).

Japanese scops owls preyed more on juveniles and subadults of all four species rodents, and Ural owls consumed more adults than juveniles of *Apodemus agrarius*, *Rattus norvegicus* and *Tamias sibiricus* (Table 3). Ural owls preyed more on juveniles and subadults of *Apodemus draco*, but consumed more adults than expected (Table 3).

Discussion

Although the Ural owls (355-580 g) are larger than the Japanese scops owls (135-200 g), both preyed upon the same small rodent species (Table 2). This was probably because most prey taxa in the study site were quite small. However, the proportion of these prey in the diets differed between the two species. Rodents were frequently found in pellets of the Japanese scops owl, occurring in higher numbers per pellet and present in nearly all pellets. Thus, rodents made up the bulk of the diet in terms of both the frequency and biomass. However, these species were also the primary part of the Ural owl's diet: common in terms of biomass, although showing a lower frequency than in the diet of Japanese scops owls. The invertebrates (mainly insects), birds and small amphibians were the main supplemental prey of the Japanese scops owl. In contrast, the secondary items in the diet of Ural owl were invertebrates (mainly spiders and scorpions), snakes and small amphibians.

Differences in size and age of rodents taken by both species of owls was unlikely the result of differences in predator size ratio and handling capabilities. Although the Ural owls are substantially larger than the Japanese scops owls, both species are large relative to the prey in question. Moreover, the Japanese scops owl is capable of preying on larger species of small mammals. Our results supported the predictions of Greene (1986), who suggested that sit-and-wait predators take larger and older prey than those taken by active predators. Although both owl species preyed heavily on juveniles of *Apodemus draco*, Japanese scops owls consumed more juveniles than Ural owls. Japanese scops owls usually hunt over open areas and are able to find small mammal nests using auditory cues. According to Grant & Noakes (1987), active predators are more likely to encounter and feed on patchily distributed or sedentary prey, such as juveniles in a nest. Conversely, as predominantly sit-and-wait predators, Ural owls rely more heavily on prey movements to stimulate attacks (Greene 1986, Lesinski et al. 2008) and probably specialize on fast-moving animals (Huey & Pianka 1981, Grant & Noakes 1987). The Ural owl watches rodents from a perch or the ground, capturing and consuming small mammals, such as moving subadults and adults (Brown & Twigg 1971).

Generally, adult rodents of many species display territorial behaviour that decreases predation risk through increased knowledge of the habitat and a greater ability to escape predators (Metzgar 1967). Thus, juvenile rodents are often more vulnerable to predation than adults. However, Ural owls did not prey more on juvenile as expected. It appears instead that both owl species adopted contrasting feeding strategies. The more active owl species was more likely to catch younger and/or smaller than average individuals, a similar result as those reported from Australia (Dickman et al. 1991), Brazil (Motta-Junior 1996), Argentina (Trejo 2006), and Mali (Granjon & Traoré 2007). In contrast, the higher predation on subadults and/or adults compared to juveniles for Ural owls was observed in Finland (Korpimäki & Sulkava 1987).

Few studies have compared the consumption of small mammals by two owl species simultaneously. However, one study that has made such a comparison found greater consumption of adults and/or larger small mammals by barn owls (the more active species) (Derting & Cranford 1989), compared with a strong preference of juveniles by burrowing owls (the sit-and-wait predator) (Bellocq & Kravetz 1994). Further comparisons of our findings with those of previous studies are difficult due to differences in methodology: statistical analysis, trapping techniques, sample size, prey species, mass/age estimates, and age class criteria.

Leveau et al. (2006) suggested the predators may exhibit a selective diet within a particular study site, but may alter such preferences for prey of different sizes and ages across their range. Regardless, our results showed that at our study site the active predator fed on smaller and younger prey, whereas the predominantly sit-and-wait predator depended on relatively larger and older prey. We encourage researchers to use standardized protocols to better facilitate comparative studies.

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