Potential resource competition between an invasive mammal and native birds: overlap in tree cavity preferences of feral raccoons and Ural owls

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Running head: Potential competition of an invasive cavity-using mammal on native birds

Abstract

Invasive mammals include good tree climbers that use tree cavities for resting and nesting. Tree cavities are important but limited resources in most forests; thus, some invasive mammals can be serious competitors for native cavity-using species, especially cavity-nesting birds. Despite the potential impact, such inter-class competition has rarely been considered. We examined the possibility of resource competition for tree cavities between the invasive raccoon *Procyon lotor* and the native Ural owl *Strix uralensis*. Both species are nocturnal and use tree cavities during daytime. We assessed an overlap in cavity use for both species as an indication of potential competition by monitoring 341 cavities during their breeding season in a natural park in Hokkaido, Japan. Of 341 potentially available cavities, raccoons and Ural owls used 37 and 32, respectively. The characteristics of 58 cavities used by raccoons or owls were compared to 49 random cavities to determine if they selected cavities with certain characteristics. As predicted from a large amount of tree cavities and a low raccoon density in this managed forest, we did not find direct evidence of competition, such as physical interaction, intrusion to cavities, or habitat segregation. Cavity types used by both species overlapped considerably in terms of height, entrance size, depth, and other characteristics: their habitats were widely overlapped. Further, in four cavities, one species was replaced by the other. Given the similar habitat requirements, the invasive raccoon could be a potential competitor for Ural owl when raccoon density increases and/or cavity availability decreases, which is the case for many forests in Japan. This study suggests that potential threats of resource competition among not only closely but also distantly related taxa should be taken into consideration when studying the impacts of invasive species.

Keywords: alien species, habitat selection, inter-class competition, tree hollow

Introduction

Competition between invasive and native species has become a serious ecological problem throughout the world (Strubbe and Matthysen 2007; Kumschick and Nentwig 2010; Koch et al. 2012). However, most studies have focused on taxonomically related groups. Competition between distantly related taxa has been considered to a lesser extent, although several studies have suggested inter-class competition in native communities mostly between small mammals and small birds (Sará et al. 2005; Lambrechts et al. 2007; Kappes and Davis 2008; Jennings et al. 2010). Here we examined the possibility of resource competition for tree cavities between the invasive middle-sized mammal, raccoon *Procyon lotor*, and the native large cavity-nesting bird, Ural owl *Strix uralensis*.

Interspecific competition in which individuals of different species compete for limited resources should be a ubiquitous phenomenon shaping community structures, but demonstrating it in the wild is not always easy (Wiens 1989). Field manipulation, such as adding or removing putative competing species, is probably the best way but often practically and/or ethically difficult especially for invasive birds and mammals (but see Stokes et al. 2009; Strubbe and Matthysen 2009). Therefore, indirect evaluations, such as examination of distributional pattern or overlap of resource use, are often employed for the inference of competition. Exclusive distribution, negative correlations of density, and overlaps in resource use are considered as indications of resource competition (Wiens 1989). However, such patterns may change markedly even in short time scales for native and invasive species. After complete displacement by invasive species it is impossible to assess past competition. In addition, invasive and native species may co-exist by partitioning common resources (Harrington et al. 2009).

In such cases, we cannot confidentially distinguish from a snapshot of data whether the lack of overlap in resource use is due to resource partitioning (i.e. with past competition) or due to different habitat requirements for different species (without competition). Therefore, in order to assess the species overlap in resource use, habitat usage of invasive and native species should be examined in an area where resources are not currently limited. To do so, we can provide the basic information of habitat preference of invasive species to infer potential competition to native species.

Tree cavities are important but limited resources that influence forest biological diversity (Newton 1998; Martin and Eadie1999; Cockle et al. 2011). Cavities are used by many animals including mammals, birds, amphibians, reptiles, and insects, as resting, breeding, feeding, and hiding sites (e.g. McComb and Noble 1981; Martin and Eadie1999; Gibbons and Lindenmayer 2002). For example, 31% of mammal species in Australia and 12% of bird species in four continents (Europe, North America, South Africa, and Australia) use tree cavities (Newton 1998; Gibbons and Lindenmayer 2002). Therefore, a lack of suitable cavities often imposes strong competition (Ingold 1998; Poonswad et al. 2005) and even regulates population sizes (Newton 1998).

Competition for tree cavities between native and invasive species has been reported for some bird species (Koenig 2003; Strubbe and Matthysen 2007, 2009). Invasive mammals could also influence native bird communities by competing for cavities because they include good tree climbers, such as the common brushtail possum *Trichosurus vulpecula* and stoat *Mustela erminea* (ISSG 2012), which use tree cavities as resting and breeding sites (hereafter, we use the term “den sites” to indicate both resting and breeding sites). In native communities, such inter-class competition has often been suggested for cavity-nesting birds and small mammals such as mice and squirrels (Sará et al. 2005; Lambrechts et al. 2007; Kappes and Davis 2008). However, potential competition between invasive mammals and native birds has been rarely investigated (but see, Matsui et al. 2009), although the threat of nest predation (i.e., to eggs or chicks) by invasive mammals has often been reported (e.g. Brown et al. 1993; Wilson et al. 1998). Even without direct need for nest predation, frequent visits of mammals that climb trees to find den sites may disturb bird species especially during breeding seasons, given that sensitivity of breeding birds to human visits is often associated with nest abandonment (e.g. Richardson and Miller 1997).

The feral raccoon *Procyon lotor* is one of the mammals that utilize tree cavities as den sites. They can climb trees as high as 35m (Bartoszewicz et al. 2008). In their native range, tree cavities account for approximately 40% of the raccoons' den sites throughout the year and greater than 90% for females during the breeding season (Wilson and Nielsen 2007; Smith and Endres 2012). In addition, this species has relatively low site fidelity; they rarely use the same den site among seasons or even on consecutive days (Shirer and Fitch 1970; Lotze and Anderson 1979). Due to its relatively large body size, raccoons require large cavities (entrance size > 10cm;) that are generally very limited resources except in some pristine or well-preserved natural forests. Moreover, raccoon density can be very high even in their native ranges (>10-100 individuals/km^2; Wilson 2005). Therefore, raccoon may be a strong competitor for cavity-using animals.

Invasive raccoons have been introduced throughout the world from North America and have established persistent populations in many regions, including Europe, Alaska, the West Indies, and Japan (García et al. 2012). Feral raccoons were first detected in Japan in 1962 and their range has expanded over the entire region (Kaneda and Kato 2011). Several impacts on native ecosystems resulting from their invasion have been reported, including the predation of aquatic animals and attack on a reproductive colony of gray heron (Ikeda 1999; Ikeda et al. 2004; Hori and Matoba 2001; Hayama et al. 2006). Therefore, this species is included in 100 of the worst Japanese invasive alien species (Murakami and Washitani 2002).

The main objective of this study was to evaluate the potential resource competition between invasive raccoons and native cavity-nesting birds. In particular, we expected that owl species might experience a stronger influence than other cavity-nesting birds because both owls and raccoons are nocturnal and use large cavities during daytime. Therefore, we examined the degree of the overlap in cavity use between raccoons and the Ural owl *Strix uralensis*, one of the basic premises for resource competition. To clarify the natural variations in cavity use for each species we selected a study site where tree cavities were abundant and raccoon density was low. We predicted that current competition between raccoons and owls should be weak in this managed forest due to a large amount of tree cavities and a low raccoon density, which enabled us to determine the habitat preferences of both species. Based on the habitat requirement of invasive raccoon, we discuss potential interactions with native bird species in this forest as well as other forests in Japan.

Methods

Study area

We conducted field survey during 2011–2012 in the Nopporo Natural Forest Park, located 11-15 km east of Sapporo city (43°25′N, 141°32′E), central Hokkaido, Japan. The Nopporo Natural Forest Park forest is a 2,040 ha semi-isolated forest with altitudes of 30–90 m above sea level. This forest was designated as a national forest in 1873 and a prefectural natural park in1968. Natural mixed conifer-hardwood predominate the forest (1,010 ha) and there are plenty of large trees [e.g., >90 cm in diameter at breast height (DBH)] with natural cavities or cavities excavated by woodpeckers. The presence of raccoons was first confirmed in this park in 1992 (Kadosaki 1996). Largely because of the agricultural damage caused by them, great efforts have been made to eliminate raccoons since 1999 and the population has been maintained at very low densities (i.e., 0.6 individuals/km^2 in 2011: Hokkaido Prefecture, unpublished data).

Cavity usage of raccoon and Ural owl

We monitored cavities in trees along valleys because there was a large number of old trees along the valleys due to low levels of human disturbance and because raccoons prefer habitats along rivers or streams (Wilson and Nielsen 2007). The total area surveyed was approximately half of the park. We counted cavities in large trees from the ground using binoculars after leaves had fallen (January to March 2011). We tried to record all cavities with an entrance width greater than approximately 10 cm at the narrowest point, which is considered as the minimum width required for both raccoons and Ural owls (Stuewer 1943; Lõhmus 2003). All located cavities were checked whether they were large enough to contain den sites by direct observation and CCD camera (see below). To confirm the use of cavities by raccoons and Ural owls, we examined the interior of each cavity at least two times: twice during their breeding seasons (May to July 2011) and again when we measured the physical characteristics of the tree cavities (January and May to July in 2012, see below). We recorded the cavity use by direct observation or by use of a wireless charge-coupled device (CCD) camera with light emitting diodes (LEDs) installed in an aluminum tube and mounted on a 5-m telescopic aluminum pole (Matsuoka 2010). To examine the high cavities (≥ approximately 7 m), we climbed trees using single-rope and double-rope techniques (Davis 2005). Evidence of occupancy such as the presence of hair, feces, and pellets were also used to determine the use of cavities. These indicators were unique for raccoons and Ural owls in this forest (i.e., there were no equivalent indicators for other mammals or birds) and provided reliable evidence of short-term cavity use. Animals that potentially used large tree cavities in this forest were the Hokkaido squirrel *Sciurus vulgaris orientis*, Russian flying squirrel *Pteromys volans orii*, and mandarin duck *Aix galericulata*. Additionally, we collected information regarding the cavities used by each species from local observers who had reliable data such as photographs.

We measured physical properties of tree cavities used by raccoons and Ural owls to determine their external (number of suitable entrances, cavity height, entrance width, and entrance height) and internal (cavity depth, internal width, and length) characteristics (Fig. 1). If a cavity had multiple entrances, the entrance characteristics were measured for the entrance where animal signs were observed or the lowest entrance because raccoons and most nest predators, such as snakes, climb from the bottom. The entrance area (cm^2) and cavity basal area (cm^2) were calculated assuming these areas to be ellipses. We calculated the basal area using internal width and length measurements from the bottoms of the cavities where possible. If the bottom was too deep to measure these characteristics, the surface area of the cavity entrance was used. The following non-numeric characteristics of the cavities were also recorded: cavity location (branch, trunk, or fork), cavity type (cavity with a side entrance or others, such as a cavity with an upper entrance or a chimney cavity), and the origin (natural or excavated by animals such as woodpeckers). In addition to the cavities, we measured tree characteristics (i.e., height, DBH, and decay class, i.e., living or dead). Forty-nine unused cavities were randomly selected (hereafter called “random cavities”) and similarly measured as indicators of cavity availability in this forest, which we used for statistical analysis (as described below). Cavities that were difficult to approach because of the decay of the tree or their inaccessible location were measured only with respect to some measurable characteristic.

Overlap in cavity use between raccoon and Ural owl

Overlaps in cavity use between raccoons and Ural owls were assessed using the method of Petraitis (1979). This general overlap value (*G*) indicates the likelihood that the proportions of observed resource use by species *i* in each parameter category (see below) are the same as the proportions of observed resource use by species *k*:

$$G = \exp\left(\sum_{j=1}^{R} p_{ij}\ln(p_{kj}) - \sum_{j=1}^{R} p_{ij}\ln(p_{ij})\right)$$

where R is the number of categories, p_{ij} is the proportion of resource *j* usage by species *i*, and p_{kj} is the proportion of resource *j* usage by species *k*. This value ranges from zero (no overlap) to one (complete overlap). Principal components analysis (PCA) was used to summarize information of eight cavity characteristics (number of suitable entrances, cavity height, cavity depth, basal area, entrance area, cavity type, tree height, and DBH) to fewer variables (cf. Brazill-Boast et al. 2010). Due to their strong correlations, the entrance area was used to represent the entrance width and height, whereas the basal area was used to represent the internal width and length. The other characteristics (decay class, cavity location, and the origin) were excluded from analysis because there were no obvious differences among the cavity usage categories for these characteristics (Appendix 1). We used the first four principal components (PC1–PC4) for the resource overlap analysis because these four components explained 70.7% of the total variance in the cavity characteristics with their eigenvalues being more than 0.9 (Table 1). These four principal components, however, could not be interpretable as particular cavity features, such as cavity size or tree characteristics. Therefore, they should summarize some unrecognizable features. We considered that this method was still valid to compare the overlap in cavity use between raccoons and owls, even though no particular features were determined (such cavity preferences were examined in the following analysis). The value of each principal component was divided into a number of categories, which were chosen to be small enough to minimize redundancy and large enough to minimize the information loss caused by lumping (Brazill-Boast et al. 2010). Dividing the values in each variable into a number of categories was required for resource overlap analyses (Petraitis 1979) and the number categories chosen did not significantly change our results (not shown). The likelihoods of overlaps were tested using the chi-square test. The null hypothesis was complete overlap and rejecting this hypothesis indicated some or no overlap (these two cases could not be distinguished).

Cavity preferences of raccoon and Ural owl

We examined cavity preferences of raccoons and Ural owls by comparing the used cavities and random cavities with logistic regression analysis. The usage of cavities by raccoons or owls was used as the response variable and the eight cavity characteristics (number of suitable entrances, cavity height, cavity depth, basal area, entrance area, cavity type, tree height, and DBH) as explanatory variables. Multicollinearity between the explanatory variables was assessed using the variance inflation factor (VIF) and was not detected (i.e., VIF < 2.0). Model selection was conducted using Akaike's information criteria (AIC). The model with the smallest AIC was defined as the best fitted model. Fitted values were calculated on the basis of coefficients estimated from the selected model (Fox 2003; Fox and Andersen 2006). The fitted values represented the probability of usage of the cavities by raccoons or Ural owls relative to each explanatory variable, simplifying the interpretation of the relationship between cavity usage and characteristics. All statistical analyses were conducted using R software version 2.10.2 (R Development Core Team 2010).

Results

Cavity usage and characteristics

We detected 383 tree cavities and found that 341 cavities were considered to be potentially suitable (i.e. large enough to contain den sites). Of the 341 cavities, 70 were used by animals (i.e., an occupancy rate of 20.5%) including 37 by raccoons (10.9%), 32 by Ural owls (9.4%), 2 by Mandarin ducks (0.6%), and 3 by unknown species (nest materials observed, 0.9%). Of the used cavities, 4 had been used by both raccoons and Ural owls. In one of these cavities, Ural owls had nested until 2006, although it was replaced by raccoons in 2007 (Fig. 2a and 2b). Another cavity contained raccoon hair in 2011 but was nested by an Ural owl in 2012. The remaining 2 cavities were determined on the basis of reports from local observers and indirect evidence (i.e., Ural owl pellets and raccoon hair). The 70 used cavities were natural cavities (i.e., not excavated) located in trunks but not branches (Appendix 1). All of the used cavities occurred in live trees except for one cavity used by a raccoon in a dead tree.

We measured the characteristics of 107 cavities, including 58 cavities used by raccoons and/or Ural owls and 49 random (unused) cavities (Table 2 and Fig. 3). Raccoons and Ural owls used a wide variety of cavities, particularly in terms of cavity height and depth (Fig. 3a and 3c). Raccoons used cavities that measured 0–590 cm in depth and 0.4–17.9 m in height. Ural owls used cavities that measured 0–890 cm in depth and 3.0–18.8 m in height. In addition, raccoons used cavities with the minimum entrance width (i.e., only 8 cm). Most of the parameters widely overlapped between raccoons and owls as well as between used and random cavities (Table 2 and Fig. 3).

Overlap in cavity use

The overlap in cavity characteristics used by between raccoons and Urals owls was very high for PC2 (G = 0.91, P = 0.333) and PC3 (G = 0.892, P = 0.249) (Table 1). The G values for PC1 and PC4 were significantly different, although they were still high (G = 0.831, P = 0.002 for PC1; G = 0.885, P = 0.012 for PC4).

Cavity preferences of raccoon and Ural owl

For both raccoons and Ural owls, there were up to 8-9 candidate models that supported the notion that the cavity used were not a random subset of available sites. Most models were within ΔAIC < 2.0 of the best fitted model except the full models and null models, for which there was no support (Table 3 and 4). For raccoons cavity depth and basal area were always selected by the models where ΔAIC < 2.0. The best fitted model indicated that the probability of usage by raccoons was higher in deeper cavities with a larger basal area, although the probability was relatively high (>0.3) even in shallower cavities with a smaller basal area (Fig. 3 and 4). Cavity usage of Ural owl was explained by cavity height, cavity depth, and DBH (Table 4). These variables were always selected by the models where ΔAIC < 2.0 except for one case. The probability of usage by Ural owl was higher in deeper cavities, in cavities located in higher positions, and cavities in trees with larger DBH (Fig. 5). However, similar with raccoons, cavity use of Ural owls was not very strict, sometimes using shallow cavities or cavities in lower positions (Fig. 3 and 5).

Discussion

To verify interspecific competition is generally difficult and there are several approaches with variable strengths of evidence (Wiens 1989). In this study we used one of the basic and indirect approaches (i.e. overlap in resource use) to examine potential resource competition between relatively large invasive mammal and native bird. As predicted from the great number of tree cavities and a low density of invasive raccoons in the study site, cavity occupancy was not high both for raccoons and native Ural owl and the patterns of cavity usage widely overlapped. This confirmed that the competition for cavities was currently weak and the observed pattern of cavity use represented the preference of each species. The similar habitat requirements also suggested that the invasive raccoon could be a potential competitor for Ural owl under some conditions. We discuss from our data about when and in what situations invasive raccoons can become actual competitors for Ural owls and other native cavity-using animals.

At present, resource competition between raccoons and Ural owls should be weak in this preserved forest but it could become significant if the abundance of invasive raccoons increases and/or suitable cavities decreases. Other forests in Japan may be in such situations. Large trees with large cavities are still abundant in the Nopporo Natural Forest Park but have decreased in other Japanese forests due to deforestation, loss of natural forests, and selective logging of cavity-bearing trees over the past century (Yanagawa and Muraki 2005; Japan Forestry Agency 2010). In addition, the density of raccoons in other areas is much higher. For example, raccoon density in Chiba prefecture was 2.0–11.0 individuals/km^2 (Asada and Shinohara 2009), which is 3-20 times higher than that in the study area. Nevertheless, this density could become even higher in the future considering that normal densities in its native range are generally more than 10 individuals/km^2 and can be greater than 100 individuals/km^2 (Wilson 2005). Given that 10% of the cavities in our study forest were used by raccoons even under such a low density (0.6 individuals/km^2), raccoons might already have some impact on owls and other cavity-using species in other typical (degraded) areas. A similar survey must be conducted in areas where raccoons occur at higher densities and/or where cavity availability is limited.

The actual availability of tree cavities may be more limited than that observed in this natural park. We measured the physical characteristics of the cavities but not their microclimates (e.g., temperature and humidity) that may also influence cavity selection (Newton 1998). This may be particularly important in winter with snow cover from early-December to early-April and where temperatures drop below -10℃ in this area. Therefore, availability of cavities may decrease in winter, the season when raccoons become highly dependent on tree cavities (Wilson and Nielsen 2007; Smith and Endres 2012). Seasonal and regional climate may influence the interaction between raccoons and owls.

What is critically lacking is the knowledge about direct physical interactions. In several cavities, Ural owls were replaced by raccoons and vise versa. This could be attributed to raccoons taking over owl's cavities, but simply owls might have moved to other cavities and then, raccoons used the abandoned ones. Ikeda (2004) noted a takeover of an owl's cavity nest by a raccoon but did not present any direct evidence. It may be difficult for raccoons to take over owl's nest cavities because breeding females of Ural owls are extremely aggressive devoting much cost to protect offspring (Kontiainen et al. 2009). Although challenging, recent development of animal tracking video systems might provide some information about direct interspecific interactions (e.g. Moll et al. 2007).

Raccoons had a wide resource use, suggesting that they use tree cavities opportunistically. Robb et al. (1996) also reported that characteristics of cavities that were used and unused by native raccoons were similar. This indicates that invasive raccoons would potentially affect various native cavity-users other than Ural owl, such as Mandarin ducks and squirrels, when availabilities of cavities are restricted. On Hokkaido Island, our special concern is the Blakiston's fish owl *Ketupa blakistoni,* a critically endangered species (IUCN 2012). Raccoons recently invaded one of the few remaining habitats of Blakiston's fish owl (Murakami and Washitani 2002). This one of the largest owl species requires large tree cavities with a basal area of more than 1590 cm^2 (Takenaka 1999), which overlaps with the raccoon's range (325–3843 cm^2). Such large cavities are very scarce in these habitats and approximately 40% of breeding pairs use artificial nest boxes (Takenaka 1999). Therefore, special attention should be paid to prevent raccoons from invading the fish owls' habitats.

Opportunistic habitat use by raccoons, on the other hand, might mitigate resource competition with native species. Raccoons might be able to partition tree cavities with various species, thereby allowing long-term co-existence. If this is true, restoration of tree cavities would reduce potential interactions with native cavity-nesting species.

Conclusion

The effects of invasive mammals have been studied mainly in the context of competition with similar-sized mammals (Abe et al. 2006; Lambrechts et al. 2007; Harrington et al. 2009), as well as predation on small animals such as birds or insects (Mitchell and Beck 1992; Hilton and Cuthbert 2010). Here we investigated a possibility of resource competition between invasive mammals and native birds. Such competition might occur for other tree-climbing invasive mammals, such as possums, weasels, squirrels, and mice. Or, conversely, invasive cavity-nesting birds might compete with native cavity-using mammals. In addition, smaller cavity-using animals, such as insects, reptiles, and frogs, could suffer from exploitative competition from invasive mammals and birds. For appropriate conservation and management, we should pay more attention to such inter-class competition.

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Figure legends

Fig. 1 Illustrations of a cavity showing the characteristics measured.

Fig. 2 a, b. A cavity used by both Ural owl and raccoon. After its use by an Ural owl as a roosting site (a), a raccoon used the cavity as a daytime resting site (b).

Fig. 3 a–d. Box plots of the characteristics of cavities used by raccoons and Ural owls and random (unused) cavities: (a) cavity height (m); (b) cavity depth (cm); (c) entrance area (cm^2); and (d) basal area (cm^2).

Fig. 4 a, b. Probability of cavity usage by raccoons relative to (a) the cavity depth (cm) and (b) basal area (cm^2) according to the best fitted logistic regression model. The dashed line represents 95% CI and short bars on the horizontal axis represent the marginal distribution of the predictor.

Fig. 5 a-c. Probability of cavity usage by Ural owls relative to (a) the cavity height (m), (b) cavity depth (cm), and DBH (cm) (b) according to the best fitted logistic regression model. The dashed line represents 95% CI and short bars on the horizontal axis represent the marginal distribution of the predictor.

Fig. 1

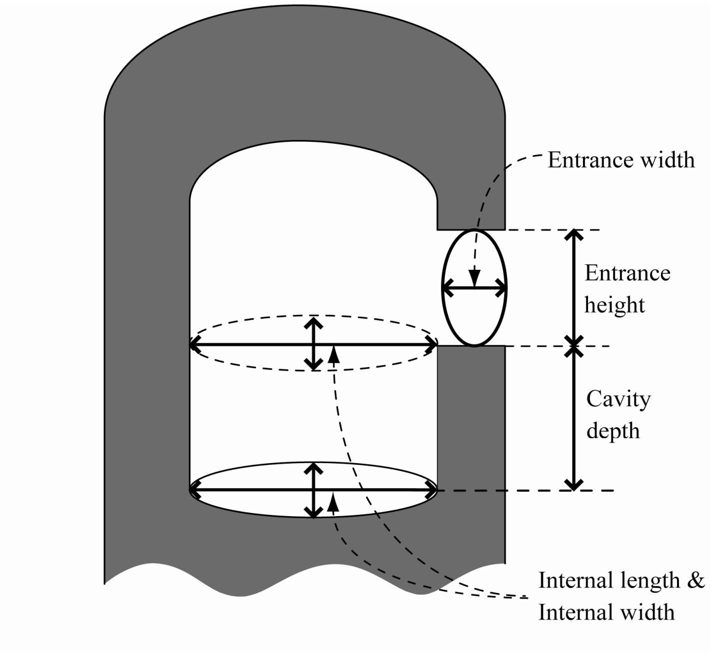

Entrance width
Entrance
height
Cavity
depth
Internal length &
Internal width

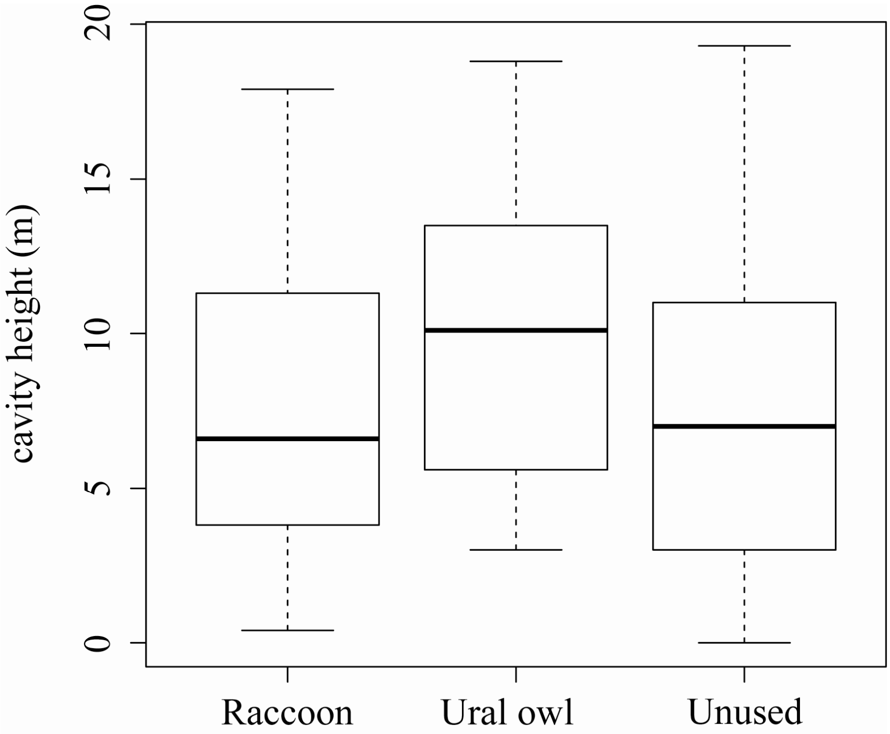
Fig. 2

(a)

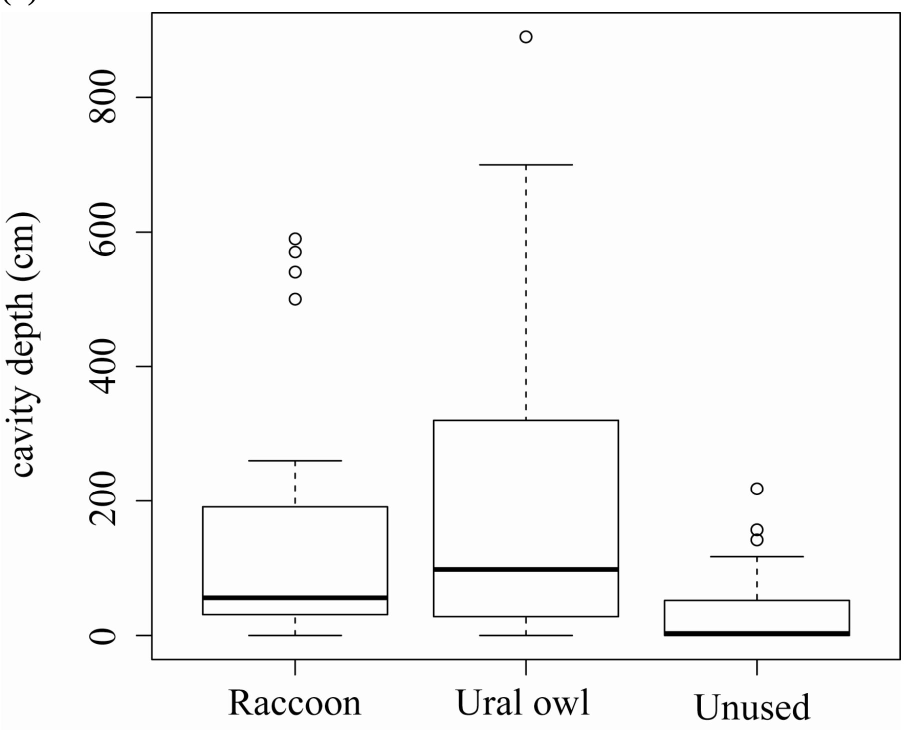
(b)

Fig. 3

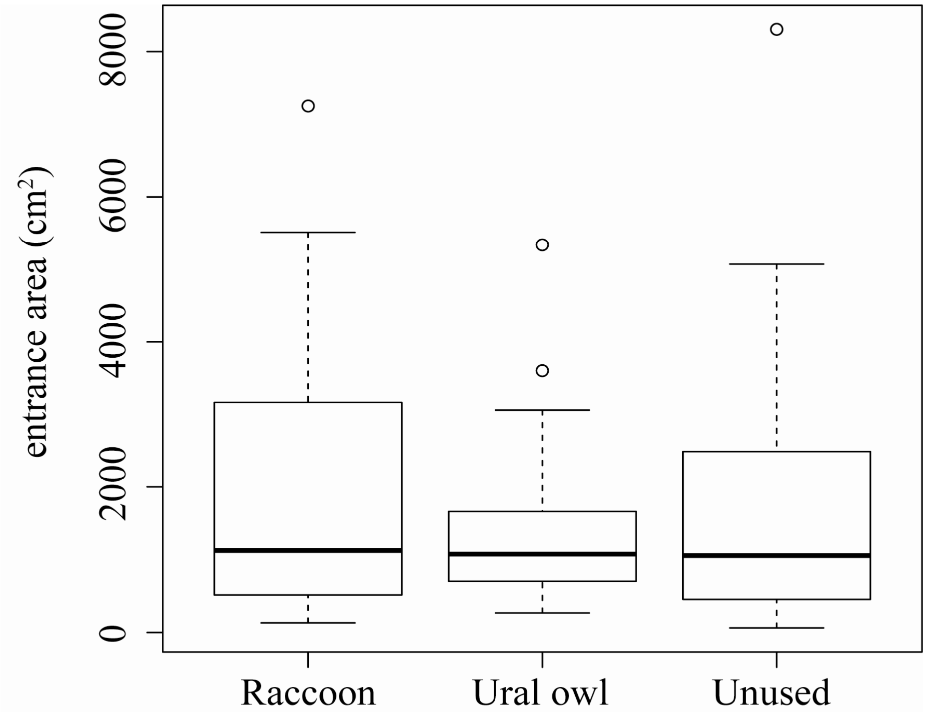
(a)


cavity height (m)
0
5
10
15
20
Raccoon
Ural owl
Unused

(b)


cavity depth (cm)
0
200
400
600
800
Raccoon
Ural owl
Unused

(c)


entrance area (cm^2)
0
2000
4000
6000
8000
Raccoon
Ural owl
Unused

(d)

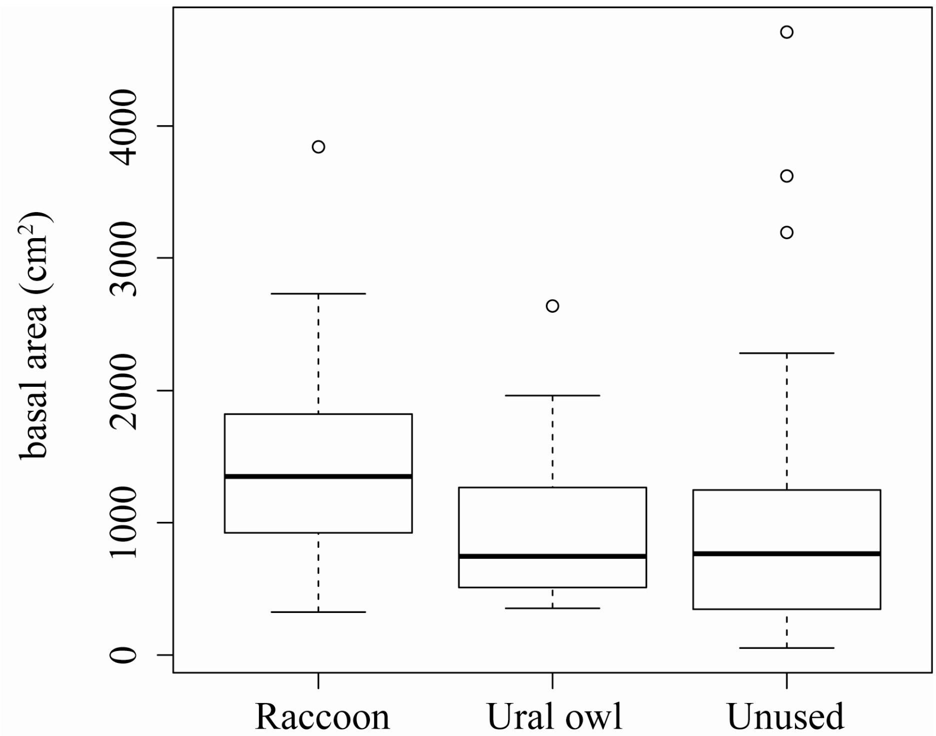
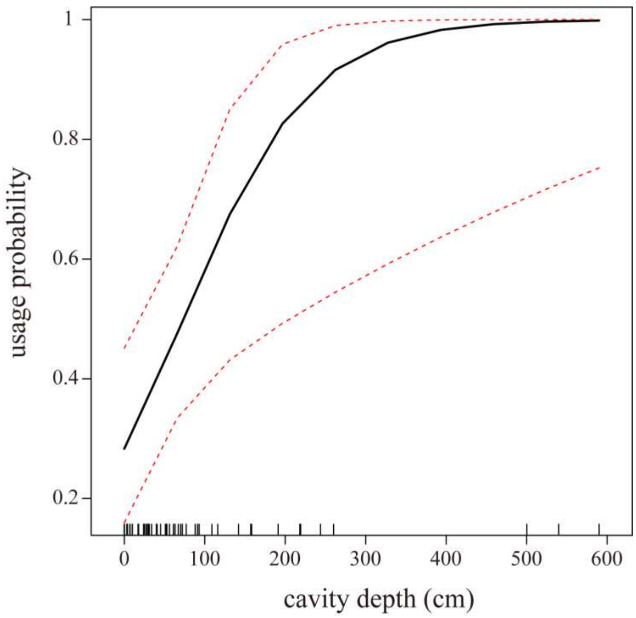

basal area (cm^2)
0
1000
2000
3000
4000
Raccoon
Ural owl
Unused

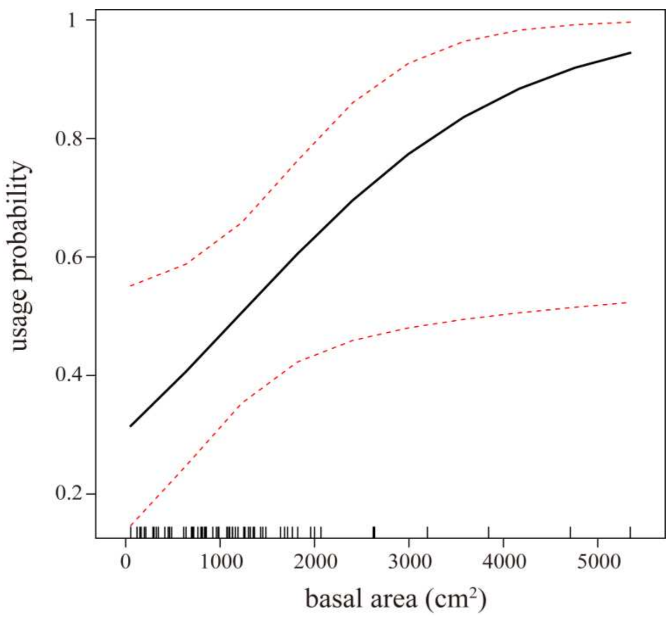
Fig. 4

(a)



usage probability
1
0.8
0.6
0.4
0.2
0
100
200
300
400
500
600
cavity depth (cm)

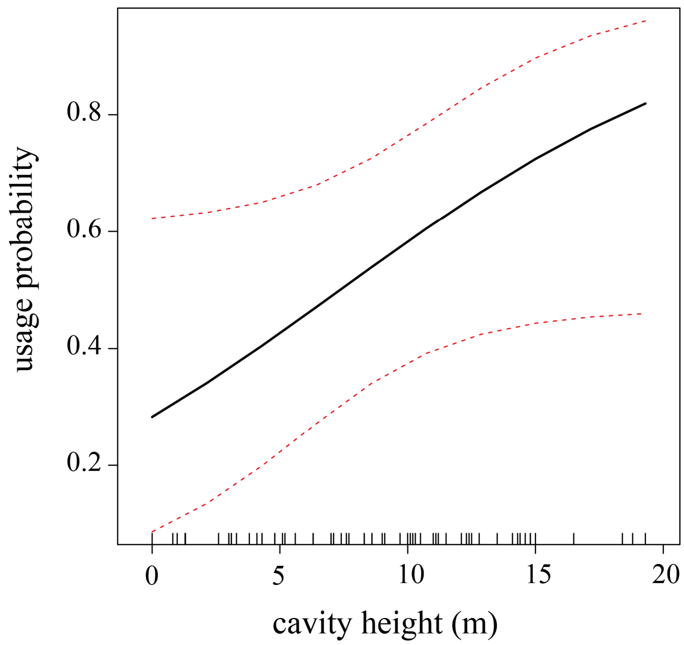
(b)



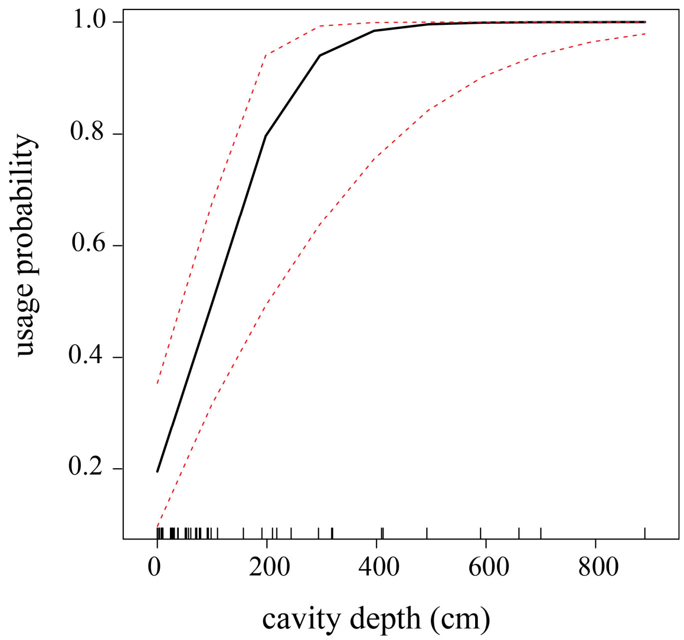
usage probability
1
0.8
0.6
0.4
0.2
0
1000
2000
3000
4000
5000
basal area (cm2)

Fig. 5

(a)


usage probability
0.2
0.4
0.6
0.8
0
5
10
15
20
cavity height (m)

(b)


usage probability
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
cavity depth (cm)

(c)

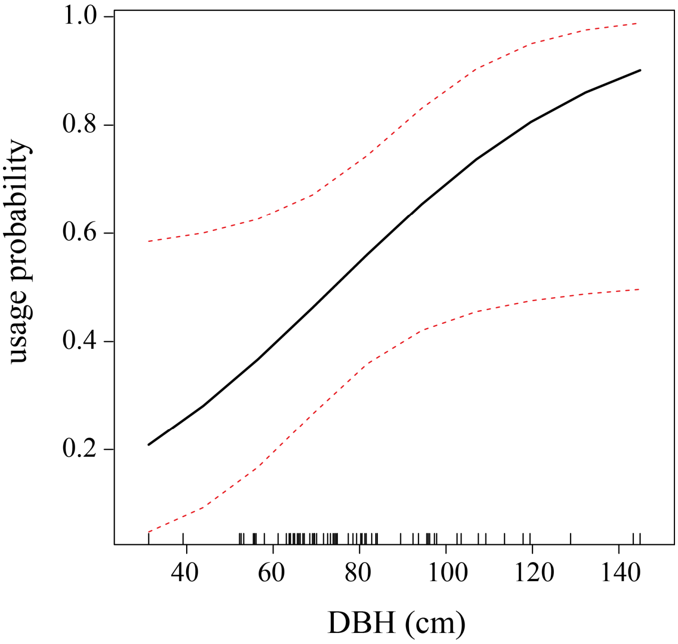


Table 1. Resource overlap (*G*) and the statistical likelihoods of the first four principal components (PC) describing cavity usage by raccoons and Ural owls. The significance levels (*P* values) based on chi-square test are also shown.

PC	Variance explained (%)	Eigenvalue	Resource overlap	
			G	*P*
PC1	25.8	2.07	0.831	0.002
PC2	19.0	1.52	0.910	0.333
PC3	14.4	1.15	0.892	0.249
PC4	11.4	0.91	0.885	0.012

Table 2. Characteristics (mean ± S.D. and range) of cavities used by raccoons, Ural owls, and random (unused) cavities. Sample sizes are shown in parentheses.

	Raccoon		Ural owl		Random	
Characteristic	mean ± S.D.	range	mean ± S.D.	range	mean ± S.D.	range
Cavity-bearing trees						
tree height (m)	19.5 ± 4.7 (32)	5.1–25.7	19.9 ± 2.9 (29)	15.0–25.5	18.5 ± 4.7 (41)	3.8–25.9
DBH (cm)	85.0 ± 22.1 (33)	49.4–149.7	85.1 ± 26.2 (29)	52.6–144.9	74.9 ± 20.1 (43)	31.2–137.3
Cavities						
number of suitable entrances	1.2 ± 0.4 (33)	1–2	1.2 ± 0.5 (29)	1–3	1.1 ± 0.4 (49)	1–3
cavity height (m)	7.7 ± 4.9 (33)	0.4–17.9	10.0 ± 4.5 (29)	3.0–18.8	7.0 ± 4.9 (46)	0–19.3
cavity depth (cm)	139.6 ± 172.8 (33)	0–590	217.1 ± 249.8 (29)	0–890	30.4 ± 48.5 (49)	0–218
entrance area (cm^2)	1889.6 ± 1784.5 (32)	131.9–7251.8	1370.7 ± 1068.1 (29)	268.5–5338.0	1626.6 ± 1657.4 (45)	63–8307
basal area (cm^2)	1498.4 ± 766.6 (33)	325.0–3843.4	965.4 ± 553.2 (29)	353.3–2637.6	998.0 ± 933.2 (49)	53–4710

Table 3. Ranking of the logistic regression models used to compare cavities used by raccoons and random cavities. The best fitted model is shown in bold. k, Number of parameters; AIC, Akaike's information criteria; ΔAIC, difference in AIC between the selected model and the best fitted model.

Variable	k	AIC	ΔAIC
cavity depth, basal area	**3**	**78.35**	**0**
cavity height, cavity depth, basal area	4	78.74	0.4
tree height, cavity depth, basal area	4	79.14	0.79
DBH, cavity depth, basal area	4	79.37	1.02
cavity depth, entrance area, basal area	4	79.77	1.42
cavity type, cavity depth, basal area	4	80.26	1.92
number of entrances, cavity depth, basal area	4	80.30	1.95
tree height, cavity height, cavity depth, basal area	5	80.33	1.98
Full model	9	88.04	9.69
Null model	1	93.74	15.39

Table 4. Ranking of the logistic regression models used to compare cavities used by Ural owls and random cavities. The best fitted model is shown in bold. k, Number of parameters; AIC, Akaike's information criteria; ΔAIC, difference in AIC between the selected model and the best fitted model.

Variable	k	AIC	ΔAIC
cavity height, cavity depth, DBH	**4**	**65.78**	**0**
cavity height, cavity depth, entrance area, DBH	5	67.10	1.31
cavity height, cavity depth, cavity type, DBH	5	67.37	1.59
cavity depth, DBH	3	67.39	1.61
cavity height, cavity depth, basal area, DBH	5	67.54	1.76
cavity height, cavity depth, tree height, DBH	5	67.66	1.88
cavity depth, entrance area, DBH	4	67.73	1.95
cavity height, cavity depth, entrance area, cavity type, DBH	6	67.75	1.96
cavity height, cavity depth, number of entrances, DBH	5	67.76	1.98
Full model	9	73.28	7.50
Null model	1	92.52	26.74

Appendix 1. Categorical characteristics of cavities.

Characteristic	Raccoon	Ural owl	Random
Decay class			
living	32	29	38
dead	1	0	6
	33	**29**	**44**
Cavity type			
side cavity	18	17	31
others	15	12	18
	33	**29**	**49**
Cavity location			
branch	0	0	3
trunk	33	29	46
	33	**29**	**49**
Cavity origin			
natural	33	29	46
excavated	0	0	2
	33	**29**	**48**