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ORIGINAL ARTICLE

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Habitat preferences of medium/large mammals in human disturbed forests in Central Japan

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Abstract It is a great concern whether human disturbed forest, i.e., secondary forest or monoculture forest, can be a habitat for the wildlife. We examined habitat preference of medium/large terrestrial mammal species in a human-disturbed mountainous settlement area of Akiyama Region, Central Japan, by using camera-traps, which were placed at conifer plantation forest, high/low-disturbed deciduous broad-leaved forest, and broad-leaved/conifer mixed forest in 2008 and 2009. Camera-traps were operational for 4568.6 trap-nights producing 740 photo-captures of 13 medium/large terrestrial mammal species. Japanese serow and Japanese hare dominated 54 % of all photo-captures. Low-disturbed deciduous broad-leaved forest showed the richest mammal fauna (12 spp.). We suggested that fruit trees and understory vegetation provided suitable habitat for frugivorous as well as herbivorous mammals. The mixed forest showed the lowest mammal fauna (6 spp.), which located higher elevation. High-disturbed deciduous broad-leaved forest (9 spp.) was also supposed to be a better habitat for some frugivorous mammals and herbivorous mammals, but tended to be avoided by Japanese marten and Japanese macaque. Conifer plantation forest (7 spp.) with understory vegetation was supposed to be a better habitat for Japanese serow and Japanese hare, but not for the other species. Without fruit trees, conifer plantation forest was supposed to be non-attractive habitat for frugivorous mammals. We demonstrated that, if a forest had been disturbed by human, the forest can be a habitat for terrestrial herbivores, but this was not always true for frugivores.

Keywords Camera traps · Human disturbance · Mammalian fauna · Conifer plantation · Occupancy model

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Introduction

Wildlife habitat destruction and fragmentation have been pointed out as the main threats to biodiversity in globally (Wilcove et al. 1998; Debinski and Holt 2000). It is thought that the massive anthropogenic disturbance to the forest by the clear cutting natural/old-growth forests or monoculture of commercial timber trees reduce the diversity of living organisms that depend on the forest, such as wildlife (Gill et al. 1996; Fitzherbert et al. 2008; Zwolak 2009). Logging has apparently a negative impact on the abundance of medium and large terrestrial frugivores (Heydon and Bulloh 1997; Gutiérrez-Granados and Dirzo 2010). For anthropogenic and natural reasons the availability of habitats has been reduced, and consequently, the proportion of individuals of certain species in a particular habitat type may be altered (Pereira et al. 2012).

Old growth forest becomes now rare in Japan as well as in the world. In need of much timber for the post-war reconstruction and the rapid economic growth in Japan, forests have changed considerably since around 1960s as a result of “expansive afforestation” [i.e., clear-felling of broad-leaved natural forests and reforesting with commercial timber conifers, such as sugi cedar (*Cryptomeria japonica*), hinoki cypress (*Chamaecyparis obtusa*), or larch (*Larix kaempferi*)]. About 40 % of Japanese forests have been converted to artificial coniferous forests (10 million ha; Forestry Agency 2000). These tree species do not provide foods for most indigenous vertebrate species, which is believed to affect Japanese wildlife significantly (Hanya et al. 2005). Most of the remaining old growth forests are valuable for the wildlife habitats. It should be widely concerned whether human disturbed forest, such as secondary forest or monoculture forest, can be a habitat for the wildlife. Therefore it is important to document the presence and the diversity of mammals occurring in various forest patches in the human disturbed landscape. Although the researches into the presence and the distribution of species are crucial for planning and evaluating conservation strategies within region (Tobler et al. 2008), those are poorly known for most terrestrial mammal species under human disturbed vegetation. This is particularly worrying for wildlife conservation and habitat management.

Camera-trapping method is increasingly used to mammal inventories, activity patterns analyses, nest ecology, behavioural ecology, habitat preference analyses and population estimation (Giman et al. 2007; Tobler et al. 2008; Kitamura et al. 2010; O'Connell et al. 2011). We conducted a 2-year camera-trap study in a human mediated landscape to document the mammalian fauna in Akiyama Region, Central Japan. This study aimed (1) to document the presence of medium/large terrestrial mammal species in a mountainous settlement area of Akiyama region, and (2) to examine their basic habitat preferences in the human mediated landscape.

Methods

Study area

The Akiyama region (138.66N, 36.85E) includes several human settlements (ca. 730 to 970 m a.s.l.) along the Nakatsugawa River valley between Mt. Naeba (2145 m a.s.l.) and Mt. Torikabuto (2037 m a.s.l.) at the boundary between Nagano and Niigata Prefectures in central Japan (Inoue 2002). The local people of Akiyama have historically used the surrounding forests for slash-and-burn cultivation, hunting of Asiatic black bear or Japanese hare, gathering of ca. 63 species of edible plants and 26 species of edible fungi, and timber extraction (Inoue 2002). Forests had been conserved since at least the middle of the Edo period (ca. 18th century; Sirouzu 2011). After the rapid economic growth in Japan (ca. 1954–1973), slush-and-burn cultivation fields were abandoned, some of which became secondary broad-leaved forests and others were modified into conifer plantation. However, some of the National forests around Akiyama Region, as well as all over Japan, had converted to the monotonous conifer plantation.

The study area was established in a 5.5 × 4 km area at approximately 675–1540 m a.s.l., extending from the bank of the Nakatsugawa River to the middle of Mt. Naeba, including the two settlements of Koakazawa and Uenohara. According to data (1979–2000) from the Nozawa-Onsen local meteorological observatory (138.44N, 36.92E) located at 576 m a.s.l. about 20 km from the study area, the mean annual temperature at the observatory is 10.5 °C, and mean annual rainfall is 1899.9 mm (Japan Meteorological Agency, http://www.jma.go.jp/jma/indexe.html). Given that the lapse rate is 0.6 °C per 100 m in elevation and we adopt temperature data of the nearest observatory, the mean annual temperature can be estimated as 9.2 °C around the settlements (ca. 800 m a.s.l.) and 1.1 °C at the top of Mt. Naeba (2145 m). Substantial snowfall occurs in winter, up to a maximum depth of about 3–4 m (Wang et al. 2008).

The vegetation of the study area exhibits vertical variation (Ishizawa et al. 2003; Tsujino and Yumoto 2013). Below 1400 m, the forests consist of natural and secondary deciduous broad-leaved forests and conifer plantations of sugi cedar *Cryptomeria japonica* or the deciduous conifer *Larix kaempferi*. Forests located at 1300–1550 m are characterised as mixed conifer and broad-leaved forests. *Abies mariesii*-dominated natural forests occur from 1500 to 1900 m. A high plain (ca. 4 km^2) of grassland and/or wetland vegetation occurs near the top of Mt. Naeba-san consisting mainly by herbs or dwarf bamboo (*Sasa kurilensis*).

In this study area, main anthropogenic forest disturbance factors were slash-and-burn cultivation, forest logging and plantation of conifers (Tsujino and Yumoto 2013). However slash-and-burn cultivation had been ceased around the 1960s (Sekido 2012), and the vegetation of abandoned cultivation fields had been shifted to typically *Betula platyphylla* var. *japonica* tree forests or young broad-leaved trees forests lacking large or old trees. Otherwise, abandoned cultivation fields had been transformed to conifer plantation. As for forest logging in the natural forest, we could find several logging stamps, if the forest logging had been conducted in the near past.

Vegetation types around settlements were classified into five categories, according to Ishizawa et al. (2003), Osumi et al. (2003), Fukushima and Iwase (2005), and Tsujino and Yumoto (2013). When the canopy trees were consisted mainly by *Cryptomeria japonica* or *Larix kaempferi*, the forest was defined as conifer plantation (CP). In the conifer plantation forests, canopy forming trees were almost same size with few medium trees but rich forest floor vegetation. When the canopy trees were consisted mainly by *Betula platyphylla* var. *japonica* or young broad-leaved trees lacking old or thick trees owing to the past human disturbance, the forest was defined as a high-disturbed deciduous broad-leaved forest (DBH). When the canopy trees consisted mainly of deciduous broad-leaved canopy trees, such as *Fagus crenata*, *Quercus crispula*, *Acer pictum* subsp. *mayrii*, *Aesculus turbinate*, or *Pterocarya rhoifolia*, and the forest was minimally disturbed by humans, the forest was defined as a low-disturbed deciduous broad-leaved forest (DBL). A forest with a canopy composed primarily of deciduous broad-leaved canopy trees (e.g., *Fagus crenata*) and evergreen coniferous canopy trees (e.g., *Tsuga diversifolia*, *Thuja standishii*, and *Pinus parviflora* var. *pentaphylla*) was defined as a broad-leaf/conifer mixed forest (BCM). The other type of vegetation was defined as the other vegetation (OTH), which included abandon paddy field and pond-side fen.

To examine the canopy tree species composition among the four forest types, i.e., CP, DBH, DBL, and BCM, in the study area, 326 transect plots (each 4 m wide × 10 m long) were established. We set 70 plots in CP, 40 plots in DBH, 196 plots in DBL, and 20 plots in BCM. Detailed methods were indicated in Tsujino and Yumoto (2013). Canopy tree species was identified in each plot (4 × 10 m). After canopy tree species were identified, we calculated the species occurrence percentage. All nomenclature followed that of Yonekura and Kajita (2003).

Camera traps

Between June and October 2008 and between June and October 2009, we deployed commercially available built-in infra-red motion sensor and flash camera units (Fieldnote II, Marif Co Ltd., Japan), in which all photographs were stamped with date and time. Colour print film (ISO 400) was used in each camera. Camera-traps were placed at 30 locations in 2008, which included 6 locations in CP, 4 in DBH, 13 in DBL, 3 in BCM, and 4 in OTH and at 30 locations in 2009, which included 6 locations in CP, 4 in DBH, 15 in DBL, 4 in BCM, and 1 in OHT in 2009 (Fig. 1). To avoid camera broken by winter snow and severe weather, we removed all camera from November to May. In 2009, we set some cameras at different locations of 2008. The mean elevation of the camera location was 1040.5 ± 224.4 m a.s.l. (675–1596 m). We checked and filled films and batteries every ca. 1.5 month. All cameras were placed on trees ca. 1 m above the ground. Camera trapping effort (number of 24 h operational camera trap nights) at each location was calculated from the date the camera was set until the date it was retrieved or, if cameras ran out of film, until the date stamped on the final exposure. The number of camera trap nights per location varied between 11.6 and 126.9 (mean ± 1SD = 76.1 ± 32.2). For all photo-captured mammals, the species, camera-trap location, date and time were recorded, however we did not include small mammals (e.g., rats, squirrels) and un-identified species, together with arboreal species (e.g., squirrels, bats) as target species. Successive photographs of the same species were defined as independent when separated by more than 30 min (Yasuda 2004).

Habitat preferences

Although there is evidence for a linear relationship between relative abundance indices (RAI: the number of independent photographs of each species per 100 camera-trap nights) and abundance estimates for ungulates (O'Brien et al. 2003; Rovero and Marshall 2008), using uncalibrated RAI for ecological or conservational studies are becoming controversial. Non-detection of a species at a site does not imply that the species is absent unless the probability of detection is 1 (Mackenzie et al. 2002). Mammals may often remain undetected within a sampling unit even if present (i.e., 'false absences'). Therefore, in order to overcome this methodological flaw in estimating abundance when detection probabilities are supposed to be < 1, occupancy can be a surrogate for abundance.

The occupancy model implements likelihood-based methods developed by Mackenzie et al. (2002) which simultaneously examine the probability of species detection and site occupancy. Occupancy analysis is well suited to camera trapping data, because detection data can be collected over a greater number of sampling occasions than through other methods such as counts of signs or sightings (Rovero et al. 2013). The occupancy model provides a flexible framework enabling covariate information to be included and allowing for false absences (Mackenzie et al. 2002). False absences are cor-

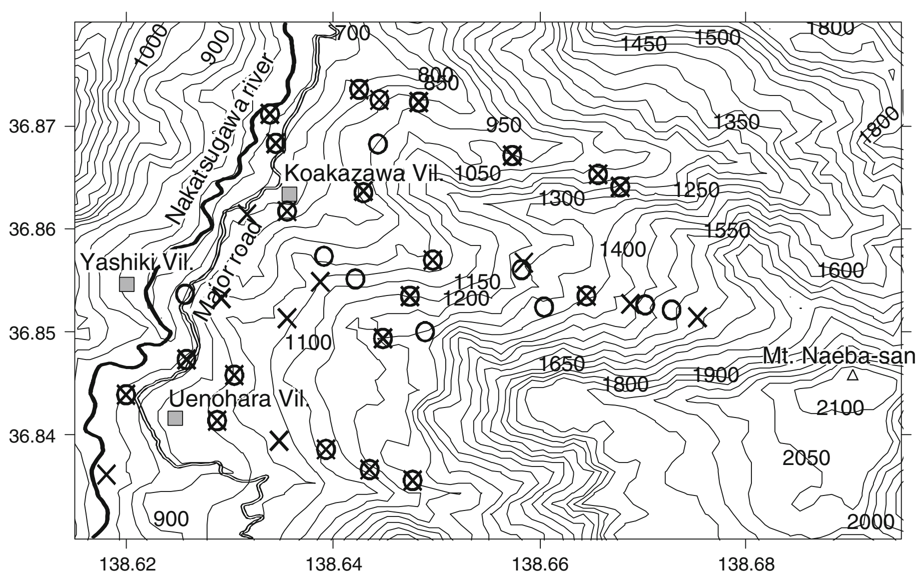

Fig. 1 Study area and locations of camera traps fixed in 2008 (*cross*) and 2009 (*circle*)

rected by conducting replicated surveys within a camera-trap location thereby allowing estimation of the probability of detecting at least one individual of a species during a survey given its presence (Mackenzie et al. 2006). In the occupancy modelling, these are essentially two nested binomial logistic regressions whereby the first models the true presence and absence of a species (site occupancy, ψ) and the second models detection and non-detection conditional (detection probability, P) on a species being present (Gray 2012). Habitat covariates can be built into reduce variance in the estimated detection probability and occupancy (Mackenzie et al. 2006). Software Presence (Hines 2014) estimates detection probability (P) and proportion of sites occupied (site occupancy ψ) assuming that sites are closed to changes in site occupancy at the species level during the study, species are not detected if they are absent, and detection at one site is independent of detection at all other sites (Mackenzie et al. 2006).

We divided the study duration by every 10-night periods starting from 18-Jun-2008, when 30 camera traps were ready to start. We defined sampling occasions as the 10-night periods, which included 10 operating days. For example, a camera operating for 34 days, non-operating for 2 days and operating for 20 days would result in 3 + 1 sampling occasions with ignoring 16 days. We set 1 for the occupancy value if the species was observed on a certain sampling occasion; 0 if the species was not observed; and NA if a sampling occasion was ignored (Ahumada et al. 2011). The mean number of sampling periods per camera-trap location was 6.2 (SD = 3.2; range 0–12). Occupancy estimates (ψ) were obtained for species that had more than ten sampling occasions among target mammal species.

Occupancy models were developed in software Presence v.3.1 (Hines 2014). Two occupancy models (ψ habitat; ψ dot) were built for each target species with habitats, CP, DBH, DBL or BCM, at each camera-trap location included as a covariate affecting occupancy. Detection probability (P) was set as constant between habitats for each species and occupancy (ψ) allowed to differ between habitat types (ψ habitat model) or set as constant across habitats (ψ dot model). Akaike information criterion values (AIC) were used to rank the two candidate models and calculate Akaike weights.

Results

Canopy tree composition

We found 11 canopy tree species in CP, 16 species in DBH, 32 species in DBL, 9 species in BCM, and 42 species in total (Appendix 1). In the CP plots, *Cryptomeria japonica* (67.1 % of plots) and *Larix kaempferi* (24.3 %) showed quite high occurrences, while other tree species showed low occurrences (< 10 %). In the DBL plots, *Betula platyphylla* var. *japonica* (47.5 %), *Quercus crispula* (42.5 %), and *Alnus hirsuta* var. *sibirica* (12.5 %) showed more than 10 % of the plots. In the DBL plot, *Fagus crenata* (50.0 %), *Quercus crispula* (24.0 %), *Aesculus turbinate* (13.8 %) and *Pterocarya rhoifolia* (10.7 %) showed more than 10 % of the plots, while the other 28 tree species showed low percentages. In the BCM plots, *Thuja standishii* (55.0 %), *Fagus crenata* (55.0 %), *Tsuga diversifolia* (35.0 %), *Quercus crispula* (20.0 %), *Pinus parviflora* var. *pentaphylla* (15.0 %), and *Tilia japonica* (10.0 %) showed more than 10 % of the plots, while the other 3 species showed low occurrences.

Mammalian fauna

Camera-traps were operational for 4568.6 trap-nights and 371 sampling occasions producing a total of 724 independent encounters of 13 medium/large terrestrial mammal species plus Japanese squirrel, Japanese dwarf flying squirrel, and un-identified Chiroptera, Rodentia and other mammals. As for target species, we found 7 species in CP, 9 in DBH, 12 in DBL and 6 in BCM (Table 1). Japanese serow (*Capricornis crispus*), which is designated as the Special Natural Monument of Japan, was the most frequently encounter species (231 encounters, 32 %; Table 2). Including the second most frequently photo-captured species, Japanese hare (*Lepus brachyurus*, 153 encounters, 21 %), the top two species dominated 53 % of all photo-captures. However Chiroptera could not identify to species, since all of Chiroptera photos were out-of-focus.

The herbivorous community was represented by Japanese serow and Japanese hare, accompanying a few

Table 1 The number of photo capture, number of species, number of camera traps and trap-nights of camera-traps

Vegetation	Photo-captures	Number of species	Number of camera traps	Trap-nights
CP	98	7	12	799.4
DBH	98	9	8	707.2
DBL	456	12	28	2247.2
BCM	45	6	7	544.5
Other	27	5	5	270.3
Total	724	13	60	4568.6

BCM, CP, DBH, DBL and other indicated mixed forest, conifer plantation, high-disturbed deciduous broad-leaved forest, low-disturbed deciduous broad-leaved forest, and other vegetation type (abandon paddy field and pond side fen)

Table 2 Number of photo-capture for middle/large mammal species at each vegetation types within Akiyama region

Common name	Species	Photo-capture						Target
		CP	DBH	DBL	BCM	OTH	Total	Mammal
Japanese serow	*Capricornis crispus*	44	21	148	16	2	231	Yes
Japanese hare	*Lepus brachyurus*	16	32	94	2	9	153	Yes
Bat	Chiroptera spp.	18	17	60	9	6	110	No
Japanese marten	*Martes melampus*	4	1	23	8	1	37	Yes
Raccoon dog	*Nyctereutes procyonoides*	0	7	24	0	3	34	Yes
Japanese macaque	*Macaca fuscata*	2	0	23	5	0	30	Yes
Masked palm civet	*Paguma larvata*	4	4	19	1	0	28	Yes
Japanese squirrel	*Sciurus lis*	1	4	19	0	4	28	No
Japanese black bear	*Ursus thibetanus*	1	2	20	2	1	26	Yes
Rat	Rodentia spp.	4	2	6	1	0	13	No
Japanese badger	*Meles anakuma*	0	4	6	0	0	10	Yes
Un-identified	Un-identified	3	0	3	1	1	8	No
Wild boar	*Sus scrofa*	1	2	2	0	0	5	Yes
Japanese weasel	*Mustera itatsi*	0	0	5	0	0	5	Yes
Domestic dog	*Canis familiaris*	0	2	0	0	0	2	Yes
Sika deer	*Cervus nippon*	0	0	2	0	0	2	Yes
Red fox	*Vulpes vulpes*	0	0	1	0	0	1	Yes
Japanese dwarf flying squirrel	*Pteromys momonga*	0	0	1	0	0	1	No
	Total	98	98	456	45	27	724	
	Active days	799.4	707.2	2247.2	544.5	270.3	4568.6	

CP, DBH, DBL, BCM and OTH indicated conifer plantation, highly disturbed deciduous broad-leaved forest, low disturbed deciduous broad-leaved forest, mixed forest, and other vegetation type, respectively

wild boar (*Sus scrofa*) and sika deer (*Cervus nippon*). The carnivorous community was represented by large omnivores [Japanese black bear (*Ursus thibetanus*), domestic dog (*Canis familiaris*), red fox (*Vulpes vulpes*)] and medium sized omnivores [Japanese marten (*Martes melampus*), raccoon dog (*Nyctereutes procyonoides*), masked palm civet (*Paguma larvata*, introduced species; Inoue et al. 2012), Japanese badger (*Meles anakuma*), Japanese weasel (*Mustela itatsi*)]. One primate species, Japanese macaque, was recorded. Two arboreal mammals, Japanese squirrel (*Sciurus lis*) and Japanese dwarf flying squirrel (*Pteromys momonga*) was also recorded, but we omitted those arboreal mammals in the further analysis. Chitoptera, Rodentia and un-identified mammals were also excluded from the further analysis.

Habitat preferences

Japanese serow was the most frequently encountered species recorded, summed across all camera-trap locations, from 115 sampling occasions (at 42 camera-trap locations), followed by Japanese hare (53 occasions at 26 locations), racoon dog (31 occasions at 18 locations), masked palm civet (28 occasions at 23 locations), Japanese marten (23 occasions at 15 locations), Japanese macaque (15 occasions at 8 locations) and Japanese black bear (10 occasions at 8 locations), and Japanese badger (7 occasions at 5 locations). Japanese badger was excluded from the occupancy analysis, owing to less than 10 sampling occasions.

Based on AIC scores, ψ habitat model of racoon dog was more strongly supported than ψ dot model (Table 3). As for masked palm civet and Japanese macaque, ψ dot models were supported with slight high AIC values in comparison with ψ habitat models, which indicated that ψ habitat models for these species were also important. On the other hand, ψ dot models were strongly supported for Japanese serow, Japanese hare, Japanese marten and Japanese black bear. Occupancy estimates of racoon dog were high in DBH and DBL, while almost zero in CP and BCM (Fig. 2). Those of masked palm civet were high in DBH and DBL and rather high in CP. Those of Japanese macaque were high in DBL and BCM. Those of Japanese marten were higher in DBL rather than CP, DBH and BCM. Those of Japanese black bear were higher in DBH rather than CP and DBL. Those of Japanese serow and Japanese hare were not so much different among vegetation types.

Discussion

Historical changes in mammal fauna

We supposed that Japanese serow and Japanese hare were dominant mammal species in this study area. In addition, it is notable that masked palm civets were inhabited not a little, and that few wild boar and sika deer were occurred. Two photo-captures of domestic dogs could be identified as one individual that was taken photo twice in the forest around settlement. Thus domestic dog must not be inhabited in the wild.

In "Akiyama Kikou (Record of the Journey in Akiyama region)", which was written by Bokushi Suzuki in

Table 3 Results of occupancy model analyses for camera traps conducted in Akiyama Region, Central Japan

Model	AIC	deltaAIC	AIC wgt	Naive occupancy estimate	ψ Mean	CI − 95 %	CI + 95 %	*P mean*	CI − 95 %	CI + 95 %
Japanese serow										
ψ(.)	316.78	0.00	0.852	0.77	0.87	0.69	0.95	0.39	0.32	0.46
ψ(habitat)	320.28	3.50	0.148							
Japanese hare										
ψ(.)	215.78	0.00	0.920	0.44	0.54	0.37	0.71	0.30	0.22	0.40
ψ(habitat)	220.65	4.87	0.081							
Japanese marten										
ψ(.)	109.90	0.00	0.865	0.23	0.50	0.17	0.83	0.11	0.05	0.24
ψ(habitat)	113.61	3.71	0.135							
Racoon dog										
ψ(.)	140.80	4.07	0.116	0.21	0.35	0.17	0.58	0.15	0.08	0.27
ψ(habitat)	136.73	0.00	0.884							
Masked palm civet										
ψ(.)	149.62	0.00	0.547	0.28	0.78	0.09	0.99	0.07	0.03	0.17
ψ(habitat)	150.00	0.38	0.453							
Japanese macaque										
ψ(.)	68.97	0.00	0.552	0.11	0.15	0.06	0.32	0.26	0.12	0.48
ψ(habitat)	69.39	0.42	0.448							
Japanese black bear										
ψ(.)	67.55	0.00	0.859	0.16	0.52	0.03	0.98	0.05	0.01	0.28
ψ(habitat)	71.16	3.61	0.141							

Akaike information criteria (AIC), delta AIC, Akaike weights (AIC wgt) for models ψ(.) and ψ(habitat), and site occupancy (ψ, with 95 % of CI) and detection probability (P, with 95 % of CI) of ψ(.) model for Japanese serow (*Capricornis crispus*), Japanese hare (*Lepus brachyurus*), Japanese marten (*Martes melampus*), Racoon dog (*Nyctereutes procionoides*), masked palm civet (*Paguma larvata*), Japanese macaque (*Macaca fuscata*) and Japanese black bear (*Ursus thibetanus*) were shown

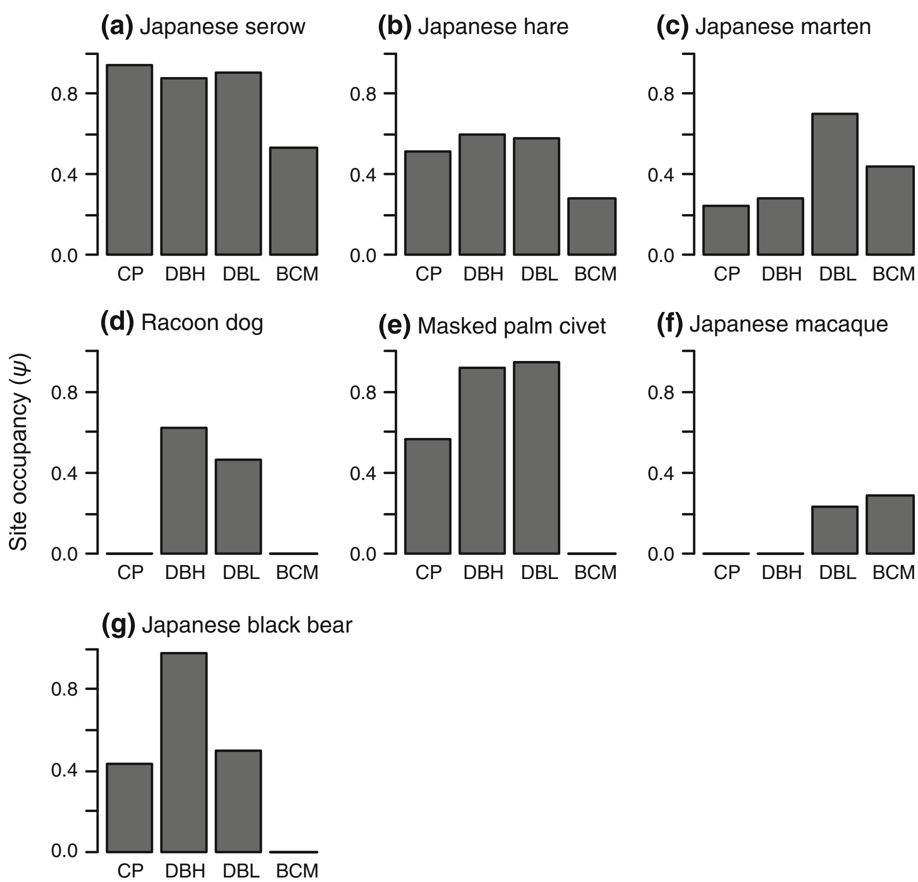

Fig. 2 Modelled occupancy estimates for Japanese serow (*Capricornis crispus*), Japanese hare (*Lepus brachyurus*), Japanese marten (*Martes melampus*), Racoon dog (*Nyctereutes procionoides*), masked palm civet (*Paguma larvata*), Japanese macaque (*Macaca fuscata*), Asiatic black bear (*Ursus thibetanus*) at camera-trap locations in conifer plantation (CP), high-disturbed deciduous broad-leaved forest (DBH), low-disturbed deciduous broad-leaved forest (DBL), and mixed deciduous broad-leaved/conifer forest (BCM) in Akiyama Region, Central Japan

1828, several mammals were listed (Suzuki and Miya 1971). Tsujino (2012) presumably identified these mammals as wild boar, Japanese macaque, Japanese black bear, sika deer, Japanese serow, gray wolf (*Canis lupus*), Japanese dwarf flying squirrel. We found all these species in 2008–2009 study, except gray wolf. Gray wolf had been extinct in Japan, after the last capture was recorded in 1905 in Nara Prefecture, Western Japan. As for Japanese serow, although heavy hunting drove Japanese serows into the high mountain (1500–2700 m) in the past, their distribution is expanding once again into lower mountains (Ochiai 2009). It may possibly that the population density of Japanese serow had been decreased in this study region from middle of Meiji era (ca. 1900s) to post-war Showa era (ca. 1960s).

Owing to the past heavy hunting, wild boar and sika deer had also almost disappeared from northern and central Honshu Island (Tsujino et al. 2010). In fact, according to the nation-wide mammalian census, conducted by Environment Agency of Japan and Ministry of the Environment (Japan) in ca. 1978 and 2000, there was no record from this study area, though there were records from Nagano Prefecture (Japan Wildlife Research Center 2004). However, these two species are now reported to be expanding (e.g., Nagano Prefecture; Koyama 2008). Although sika deer and wild boar were supposed to inhabited in this study area in the Edo period (before 1868), sika deer and wild boar had been once locally extinct before post-war Showa. After that, sika deer and wild boar came back to appearing these years.

Mammals and human disturbed forests

Modelled occupancy (ψ) ranked the species in the different order (Japanese serow > masked palm civet > Japanese hare > Japanese black bear > Japanese marten > racoon dog > Japanese macaque) as naïve occupancy estimates (Table 3). This was caused by the difference of detection probabilities among target species. For example, masked palm civet and Japanese black bear which had low detection probabilities showed relative low naïve occupancy estimates and high modelled occupancy estimates. Therefore accounting for non-detection/false-absences of focal species is an important, but traditionally often overlooked, aspect of conservation research (Mackenzie et al. 2002).

Occupancy models in this study had assumed that sites were closed to changes in site occupancy at the species level during the study. Mackenzie et al. (2006) suggested that this assumption can be relaxed provided changes in the occupancy status of sites occurs at random, with the probability of occupancy in one time interval not depending upon the occupancy status in the previous time interval. In such circumstances, ψ should be interpreted as ‘use’, as opposed to ‘occupancy’, and represents the probability of use of a site (Mackenzie et al. 2006) rather than the proportion of sites occupied (Gray 2012). Therefore, occupancy models potentially give valuable information on a species’ habitat preferences (Gray 2012).

The photo-captures and occupancies of mammals showed great variety among human disturbed/non-disturbed forest types (Fig. 2). Since the low disturbed deciduous broad-leaved forest showed the richest mammal fauna with many photo-captured mammals and high occupancies (Table 1; Fig. 2), the low-disturbed deciduous broad-leaved forest was suggested to be the most important habitat for mammals in the Akiyama Region. It was probably because the forest was consisted by *Quercus crispula*, *Fagus crenata* and other fruit tree, including sapfruits trees, i.e., *Padus grayana* and other shrubs, which provide a suitable habitat for frugivorous mammals, such as Japanese martens, Japanese macaques, masked palm civets, Japanese black bears and raccoon dogs (Torii 1986; Tatara and Doi 1994; Hanya et al. 2005; Koike et al. 2012). Dependency on broad-leaved forests of various mammals had been already reported (Japanese macaque, Izumiyama et al. 2003; Hanya et al. 2005, Japanese marten, Buskirk et al. 1996, raccoon dog; Drygala et al. 2008; Holmala and Kauhala 2009; Kauhala and Salonen 2012, badger; Holmala and Kauhala 2009). These patterns are consistent with our findings. Japanese macaque and Japanese marten also prefer the mixed forest, which located higher elevation of low-disturbed broad-leaved forest. Therefore these low-disturbed forests are suggested to be preferable habitat for those mammals.

However those frugivorous mammals avoided or less preferred the conifer plantation forest in comparison with the high- and/or low-disturbed broad-leaved forest and the mixed forest. Furthermore, as for Japanese marten, masked palm civet and Japanese macaque, they preferred the low-disturbed broad-leaved forest rather than the conifer plantation and/or the high-disturbed broad-leaved forest. Previous studies showed that *Martes* species, such as sables (*Martes americana*) and martens (*Martes zibellina*), respond negatively to the absence of tree canopy, of large live trees, and of coarse woody debris, and they prefer old-growth broad-leaved forests or mixed forests for their habitats (Buskirk et al. 1996; Potvin et al. 2000). Likewise Japanese marten in this study preferred low-disturbed deciduous broad-leaved forest and mixed forest, but did not appear to young broad-leaved forests and conifer plantation, which were lacking large live trees and enough coarse woody debris.

In monocultural conifer plantation forests of *Cryptomeria japonica* and *Larix kaempferi*, Japanese hare and Japanese serow were photo-captured many times, but not for the other species. Since conifer plantation forests are composed by commercial timber trees and provide poor fruits productions, conifer plantation forests are supposed to be less attractive habitat for frugivorous mammals. For example, Japanese macaque does nothing but pass through the conifer plantation forest (Furuichi et al. 1982). As for badger, earthworms, which are one of their main food items, are scarce in coniferous forests (e.g., Bøseth et al. 1997). On the other hand, judging from the rich forest floor vegetation (personal observation) and a lot of photos of Japanese serow and Japanese hare, conifer plantation forests are suggested to provide rich food resources with herbivores, since Japanese serow and Japanese hare feed leaves, twigs, forbs, etc. Hodson et al. (2011) showed that changes in snowshoe hares (*Lepus americanus*) abundance in boreal forest of Quebec (Canada) after post-fire and post-clearcut disturbance of the stand closely tracked changes in lateral and vertical vegetation cover, with highest faecal pellet densities observed between 40 and 50 years after disturbance. In this study area, most conifer plantation and abandonment of slash-and-burn cultivation had been taken place around 1960s (ca. 50 years before), which indicates that high-disturbed *Betura* forests as well as conifer plantations were preferable habitat for Japanese hare.

In addition, the forest floor vegetation under the broad-leaved forest is an important food resource for Japanese serow and Japanese hare, and will provide a suitable habitat for them as well. High-disturbed deciduous broad-leaved forests, such as mature *Betula platyphylla* var. *japonica* forest, which was formed by the abandonment of slash-and-burn cultivation, are also supposed to be a better habitat for those herbivorous mammal species. Thus they may tolerable to rather human disturbed forests, such as conifer plantation and/or high-disturbed deciduous broad-leaved forests in this study area.

The mammalian fauna showed great variety among human high/low-disturbed forest types. Anthropogenic forest disturbance was supposed to have reduced the mammalian diversity. However we suggested that disturbed forests were still suitable habitats for some mammal species.

Conclusion

The occupancy and habitat preference of mammals showed great variety among human high/low-disturbed forest vegetation. Japanese martens, Japanese macaques, masked palm civets, raccoon dogs and Japanese black bears preferred low-disturbed broad-leaved deciduous and/or mixed forests, while raccoon dogs, masked palm civets and Japanese black bears preferred high-disturbed broad-leaved forest as well. However those frugivorous mammals hardly utilised conifer plantation, where fruit trees are scarce. On the other hands, regrowth of logged forests and conifer plantation can be preferable habitat for herbivores, such as Japanese serow and Japanese hare. Thus we demonstrated that, if a forest had been disturbed by human, the disturbed forest may become an important habitat for terrestrial herbivores, but not always true for frugivores because of the various habitat requirements of mammals.

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Appendix 1

See Table 4.

Table 4 Canopy tree species composition of four vegetation types in 4 × 10 m plot

Family	Species	Life form	Vegetation type				
			CP	DBH	DBL	BCM	Total
Aceraceae	*Acer distylum*	DB-T	0.0	0.0	0.5	0.0	0.5
Aceraceae	*Acer japonicum*	DB-T	0.0	2.5	3.6	5.0	11.1
Aceraceae	*Acer nipponicum* subsp. *nipponicum* var. *nipponicum*	DB-T	0.0	0.0	0.5	0.0	0.5
Aceraceae	*Acer pictum* subsp. *mayrii*	DB-T	0.0	0.0	9.7	0.0	9.7
Aceraceae	*Acer rufinerve*	DB-T	0.0	0.0	1.5	0.0	1.5
Aceraceae	*Acer tschonoskii*	DB-T	0.0	0.0	0.5	5.0	5.5
Araliaceae	*Chengiopanax sciadophylloides*	DB-T	0.0	0.0	2.0	0.0	2.0
Araliaceae	*Kalopanax septemlobus*	DB-T	0.0	0.0	3.1	0.0	3.1
Betulaceae	*Alnus hirsuta* var. *sibirica*	DB-T	0.0	12.5	1.5	0.0	14.0
Betulaceae	*Alnus serrulatoides*	DB-T	0.0	0.0	1.0	0.0	1.0
Betulaceae	*Betula corylifolia*	DB-T	0.0	0.0	0.5	0.0	0.5
Betulaceae	*Betula ermanii*	DB-T	0.0	5.0	1.5	0.0	6.5
Betulaceae	*Betula grossa*	DB-T	0.0	2.5	3.1	0.0	5.6
Betulaceae	*Betula maximowicziana*	DB-T	0.0	2.5	3.1	0.0	5.6
Betulaceae	*Betula platyphylla* var. *japonica*	DB-T	2.9	47.5	3.1	0.0	53.4
Betulaceae	*Carpinus laxiflora*	DB-T	0.0	0.0	1.0	0.0	1.0
Caprifoliaceae	*Viburnum furcatum*	DB-T	0.0	0.0	0.0	5.0	5.0
Clethraceae	*Clethra barbinervis*	DB-T	0.0	2.5	0.0	0.0	2.5
Cornaceae	*Cornus controversa*	DB-T	1.4	0.0	1.0	0.0	2.4
Cupressaceae	*Thuja standishii*	EC-T	0.0	0.0	1.0	55.0	56.0
Fagaceae	*Castanea crenata*	DB-T	0.0	5.0	0.0	0.0	5.0
Fagaceae	*Fagus crenata*	DB-T	0.0	10.0	50.0	55.0	115.0
Fagaceae	*Quercus crispula*	DB-T	5.7	42.5	24.0	20.0	92.2
Hippocastanaceae	*Aesculus turbinata*	DB-T	2.9	7.5	13.8	0.0	24.1
Juglandaceae	*Juglans mandshurica* var. *sachalinensis*	DB-T	0.0	0.0	1.5	0.0	1.5
Juglandaceae	*Pterocarya rhoifolia*	DB-T	7.1	2.5	10.7	0.0	20.4
Magnoliaceae	*Magnolia obovata*	DB-T	4.3	0.0	7.1	0.0	11.4
Moraceae	*Morus australis*	DB-T	1.4	0.0	0.0	0.0	1.4
Oleaceae	*Fraxinus lanuginosa* f. *serrata*	DB-T	0.0	0.0	1.0	0.0	1.0
Oleaceae	*Fraxinus mandshurica*	DB-T	0.0	2.5	0.5	0.0	3.0
Pinaceae	*Larix kaempferi*	DC-T	24.3	0.0	0.0	0.0	24.3
Pinaceae	*Pinus parviflora* var. *pentaphylla*	EC-T	0.0	0.0	0.0	15.0	15.0
Pinaceae	*Tsuga diversifolia*	EC-T	0.0	0.0	0.0	35.0	35.0
Rosaceae	*Padus grayana*	DB-T	0.0	0.0	0.5	0.0	0.5
Rutaceae	*Phellodendron amurense*	DB-T	4.3	0.0	1.0	0.0	5.3
Salicaceae	*Salix caprea*	DB-T	0.0	5.0	1.0	0.0	6.0
Salicaceae	*Salix udensis*	DB-T	0.0	0.0	0.5	0.0	0.5
Taxodiaceae	*Cryptomeria japonica*	EC-T	67.1	0.0	0.0	0.0	67.1
Tiliaceae	*Tilia japonica*	DB-T	0.0	2.5	1.5	10.0	14.0
Tiliaceae	*Tilia maximowicziana*	DB-T	0.0	0.0	2.6	0.0	2.6
Ulmaceae	*Ulmus davidiana* var. *japonica*	DB-T	1.4	0.0	0.0	0.0	1.4
Ulmaceae	*Ulmus laciniata*	DB-T	0.0	2.5	0.0	0.0	2.5
	Number of plots		70	40	196	20	326

Values indicated mean occurrence percentage of canopy tree species in a plot. CP, DBH, DBL and BCM indicate conifer plantation, high disturbed broad-leaved forest, low disturbed broad-leaved forest, and broad-leaved/conifer mixed forest. DB-T, EC-T and DC-T indicate deciduous broad-leaved tree, evergreen conifer tree and deciduous conifer tree, respectively

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