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6 **Resource use of Japanese macaques in heavy snowfall areas: implications for**
7 **habitat management**

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21 **Abstract**

22 Populations of Japanese macaque (*Macaca fuscata*) that inhabit the northernmost
23 distribution of any non-human primates have been listed as endangered in Japan;
24 however, macaques are widely known for being pests that cause agricultural damage.
25 This study identified priority areas for the conservation and management of macaque
26 habitats, by comparing the resource use of troops occupying remote mountains
27 (montane troops) against troops inhabiting disturbed forests adjacent to settlements
28 (rural troops). We collected species presence data across two years by radio-tracking
29 two montane troops and two rural troops in the Shirakami Mountains. We developed
30 seasonal utilization distributions (UDs) by using the kernel method, and identified
31 habitat characteristics by using ecological-niche factor analysis (ENFA). Our results
32 indicate that environmental factors influencing the potential habitat varied widely with
33 season in montane troops as compared to that in rural troops. ENFA results
34 demonstrated that rural troops exhibited more biased resource use and narrower niche
35 breadths than montane troops. Based on our findings, we propose that (1) primary
36 broadleaf forests are the spring habitat conservation priority of montane troops; (2) the
37 habitat unit—the product of habitat suitability index and its surface area—for montane
38 troops is enhanced by removing old conifer plantations from the forest edge at low
39 elevations; (3) this removal around settlements may also contribute toward removing a
40 front-line refuge for rural troops intruding the farmlands; and (4) intensive prevention
41 measures against macaque intrusions into settlements during the bottleneck snowy
42 season contributes toward reducing the habitat unit of rural troops.

43 **Key words:** cool-temperate forest; habitat suitability; habitat unit; Japanese macaque;
44 seasonal range; World Natural Heritage site.

45 **Introduction**

46 Resource use of nonhuman primates often overlaps the sphere of human habitation.
47 This results in serious conflicts between local residents and wild primates—e.g.,
48 tonkean macaques *Macaca tonkeana* (Riley 2007), vervet monkeys *Cercopithecus*
49 *aethiops pygerthrus* (Saj et al. 2001), olive baboons *Papio hamadryas anubis* (Hill
50 2000), redtail monkeys *Cercopithecus ascanius*, chimpanzees *Pan troglodytes*
51 (Naughton-Treves et al. 1998). Japanese macaques (*Macaca fuscata*), which are species
52 endemic to the Japanese archipelago, are also widely viewed as serious mammalian
53 pests, causing agricultural damage in most parts of the region (Watanabe 2000; Enari
54 and Suzuki 2010; Suzuki and Muroyama 2010). However, macaque populations
55 inhabiting the northern Tohoku region, which is located in the northernmost distribution
56 of any nonhuman primate species, have been listed as endangered by the Japanese
57 Ministry of Environment since 1991 because of their segmented and isolated
58 distributions. In light of this situation, there is an urgent need to establish an appropriate
59 management protocol that serves not only to maintain these vulnerable macaque
60 population distributions but also to minimize the risk of damage caused by this species
61 to agricultural areas (Enari and Suzuki 2010).

62 Over the past half century, numerous studies have been conducted on the ecology and
63 behaviour of Japanese macaques. These studies have been mainly based on direct field
64 observations of individuals and troops (Yamagiwa 2010), including the evaluation of
65 resources specific to macaque habitats (Hanya 2010; Tsuji 2010). However, quantitative
66 assessments of habitat use by macaque troops at the landscape scale remain limited
67 (Imaki et al. 2000, 2006; Izumiyama et al. 2003). Furthermore, limited studies on the
68 resource selection function (Boyce et al. 2002) of the species, apart from a few macro-

69 scale studies focusing on multiple local populations (Enari and Suzuki 2010), have been
70 performed. The lack of information on the presence or absence of macaque troops in
71 various regions or on the resources upon which these distribution patterns depend (Enari
72 and Sakamaki 2011; Sakamaki and Enari 2012), compromises efforts to develop
73 effective habitat management plans for Japanese macaques.

74 To address the problems that many frontline managers face, this study set out to
75 identify potential priority areas for the conservation and management of macaque
76 habitats in the Shirakami Mountains, which is a continuous forested area with the
77 largest distribution of the species in the northern Tohoku region, by evaluating the
78 parameters that regulate resource use by macaque troops. These parameters are highly
79 influenced by anthropogenic factors, such as intentional artificial feeding by tourists
80 (Koganezawa and Imaki 1999) and/or the size and location of accessible croplands
81 (Imaki et al. 2000, 2006; Izumiyama et al. 2003; Muroyama and Yamada 2010). While
82 macaques have high phenotypic plasticity to gradually acclimatize to diverse
83 environments over time (Hanya 2010), they are also cautious about entering unfamiliar
84 environments (e.g., food choice, Kawai 1969; seasonal range use, Enari et al. 2006);
85 consequently, major differences in ecological, behavioural, and physiological
86 characteristics may be observed among neighbouring troops. Hence, this study
87 separately evaluated the seasonal resource uses of (1) troops inhabiting inner montane
88 forests (montane troops) and (2) troops inhabiting secondary forests adjacent to rural
89 settlements (rural troops). We then identified the similarities and differences of these
90 results for each season for the purpose of enhancing habitat quality for montane troops
91 while driving rural troops off from the area surrounding settlements. To accomplish this
92 objective, we simultaneously tracked four radio-tagged macaque troops and recorded

93 site-use. Based on this information, we calculated utilization distributions (UDs) by the
94 fixed kernel method (Worton 1989), and conducted landscape-scale evaluation of
95 macaque-habitat relationships using ecological niche modelling techniques (Guisan and
96 Zimmermann 2000; Guisan and Thuiller 2005). These techniques have been widely
97 used over the last decade to predict potential habitats by identifying suitable sets of
98 available resources for species, because model predictions are possible even in the
99 absence of extensive occurrence records (Hirzel and Guisan 2002; Pearson et al. 2007).
100 In this study, ecological-niche factor analysis (ENFA) (Hirzel et al. 2002) was used to
101 evaluate resource use by macaques within each seasonal range.

102 **Methods**

103 *Study Area*

104 The Shirakami Mountains (40°15'–40°45'N, 139°55'–140°15'E) encompass the most
105 extensive primary beech (*Fagus crenata*) forest in East Asia, with the area being added
106 to the UNESCO World Natural Heritage List in 1993 (Fig. 1). The region belongs to a
107 cool-temperate climatic zone. The mean air temperature and annual precipitation were
108 10.7°C and 1029.5 mm in 2008 and 10.6°C and 1177.5 mm in 2009, respectively
109 (public database of the Japan Meteorological Agency). The mean snow depth between
110 January and March at the local weather station located in a lowland residential area (The
111 Shirakami-Sanchi World Heritage Conservation Center) was 59.2 ± 34.5 (SD) cm (Max.,
112 107.8 cm) and 45.4 ± 22.1 (Max., 101.7 cm) in 2008. The snow depth in the
113 mountainous area generally reaches three to five times that recorded in lowland areas.
114 There was no remarkable difference in the nut production of the dominant tree species
115 (i.e., beech) during the autumn of 2008 and 2009 (Forestry and Forest Products
116 Research Institute 2012).

117 We focused on the northeastern part of the mountains. This area contains only four
118 separate macaque troops, on which our study was based. Two of the troops (troops S
119 and O) generally ranged in montane forests (montane troops), while the other two troops
120 (troops F and T) occupied rural areas (rural troops) (Enari 2007; Sakamaki and Enari
121 2012). Between 2008 and 2009, troop S had 33–37 individuals, troop O had 37–43
122 individuals, troop F had 30–34 individuals, and troop T had 29–33 individuals. The
123 mean population density (including non-troop males) in the study area was 5.19
124 individuals/km², or 0.15 troops/km², as of March 2008 (Enari and Sakamaki 2011). The
125 artificial feeding of macaques by tourists has not been observed thus far.

126 *Setting of Reference Area and Tracking Animals*

127 To evaluate the seasonal resource use by macaques, we set up a reference area that
128 was defined by a 100% minimum convex polygon of occurrence sites of the four troops
129 observed in the study (Fig. 1). While most males leave their natal groups at maturity,
130 females usually remain in their natal groups throughout their lives (Nakamichi and
131 Yamada 2010). To obtain the occurrence records, we therefore captured two, four, two,
132 and two adult female macaques from troops S, O, F, and T, respectively, by using box
133 traps (prior to February 2008 for troops S, O, and F, and prior to February 2009 for
134 troop T), and attached a radio collar (Advanced Telemetry Systems Inc.) to each
135 macaque. Next, we directly followed each troop with the aid of radio signals and
136 recorded >30 locations of the troops at >five-hours intervals (excluding night-time)
137 during each season: spring (Apr–Jun), summer (Jul–Sep), autumn (Oct–Dec), and
138 winter (Jan–Mar). In this study, the central location of the radio-tagged macaques in
139 each troop was used as the occurrence site of the troop. Troops S, O, and F were
140 observed for two years from February 2008, while troop T was observed for 1 year from

141 February 2009. The dataset included 328 occurrence sites for troop S, 333 for troop O,
142 321 for troop F, and 130 for troop T.

143 The reference area (109.6 km²) at a height of 80–900 m above sea level was located
144 in a transition zone between rural settlements and inner montane forests (Fig. 1). The
145 reference area included broadleaf forests consisting mainly of beech and oak (*Quercus*
146 *crispula*) (54.4%), conifer forests (including artificial plantations) consisting mainly of
147 Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*)
148 (28.2%), human settlements (8.4%), water bodies (5.5%), and grasslands (3.5%).

149 ***Ecological Features of Study Species***

150 Japanese macaques are forest mammals that move as troops within fixed ranges.
151 Macaques living in cool-temperate forests feed mainly on the young leaves of broadleaf
152 trees in spring, herbaceous plants and insects in summer, berries and nuts in autumn,
153 and the bark and buds of broadleaf trees in winter (Suzuki 1965; Tsuji 2010); however,
154 macaques inhabiting areas near agricultural lands may modify their diet considerably,
155 depending on crop preference (Enari 2007).

156 In general, the availability of artificial foods in rural environments may be an
157 effective factor that might reduce the spatial scale of seasonal migrations for rural troops
158 (Imaki et al. 2000), and hence seasonal range size (Koganezawa and Imaki 1999).
159 Moreover, it is widely known that, compared to montane troops, rural troops are more
160 likely to occupy conifer plantations during leafy seasons (Izumiyama et al. 2003; Imaki
161 et al. 2006), in addition to using the edge of mature coniferous plantations for cover
162 when raiding croplands (Imaki et al. 2006).

163 From 2000 onwards and 2005 onwards, troops F and T, respectively, were distributed
164 in rural areas, and raided agricultural crops throughout the year, including winter when

165 they fed on crop wastes and bark/buds of orchard trees. Troop F has been constantly
166 monitored by the authors since 2000, and was recorded to spend approximately 35% of
167 total feeding time foraging on crops (Enari 2007).

168 *UDs of Macaque Troops*

169 To evaluate the seasonal range sizes and distributions of the four different troops, we
170 calculated 95% UD by using the fixed kernel method (Worton 1989), with a smoothing
171 parameter of constant value at 500 m, using Geospatial Modelling Environment Version
172 0.5.2 beta (Beyer 2010) and ArcGIS 9.3 (Environmental Systems Research Institute,
173 Inc.). For this calculation, we used the datasets of occurrence sites described above. We
174 then calculated the UD size fluctuation range for each troop, which was expressed as the
175 ratio of maximum and minimum UD area among seasons. Furthermore, we evaluated
176 the overlapping areas of the UD among different pairs of troops by using the following
177 overlap index: $2c/(a + b)$, where a and b are the UD areas (km²) of different troops, and
178 c is the overlapping area (km²) of a and b .

179 *Data Collection for ENFA*

180 Macaque habitat preferences are mainly influenced by food resources, which are
181 determined by vegetation, climate, and topography (Iwamoto 1978; Hanya 2010; Enari
182 and Sakamaki 2011, 2012), as well as by human land use patterns, particularly the
183 distribution of agricultural lands. In areas of heavy snow, the elevation and terrain
184 conditions strictly limit macaque occurrence during winter (Enari and Sakamaki 2011,
185 2012). In addition, the locations of refuges, such as steep-sided depressions in lowland
186 areas, might protect macaques from snowstorms, and thus influence their habitat
187 preferences (Sakamaki and Enari 2012).

188 Based on these preceding studies, we initially prepared 16 environmental variables to

189 construct the model (Table 1). Five variables describing topography were calculated
190 from a digital elevation model (ground resolution = 10 m) (Geospatial Information
191 Authority of Japan 2009). Variables associated with land-use pattern (but not space-
192 scale, which cannot be incorporated into ENFA) and hydrology were obtained from
193 National and Regional Planning Bureau (2007), partly modified by high-resolution
194 satellite images (optical resolution = 2.5 m) from the Advanced Land Observing
195 Satellite (sensor name = AVNIR-2), which were taken in November 2009 (RESTEC
196 2009). Data on forest cover were obtained by digitizing analogue maps (scale, 1:5000)
197 developed for National and Private Forest Planning Maps in 2009, which were officially
198 provided by the Japanese Forest Agency and the Aomori Prefectural Government,
199 respectively. Because food abundance varies with forest age for macaques (Agetsuma
200 2007; Sakamaki et al. 2011), we decided on a threshold value of 40 years for conifer
201 forests (when the canopy becomes completely closed; Sakamaki et al. 2011) and a
202 threshold value of 100 years for broadleaf forests (when they can be roughly regarded as
203 primary forests in the absence of artificial disturbances). Because only environmental
204 variables that have continuous values (i.e., frequency datasets) can be used in ENFA
205 (Hirzel et al. 2002), we converted variables with Boolean values (i.e., presence or
206 absence) by calculating the mean value for each variable within a circular moving
207 window with a 500-m radius by using ArcGIS 9.3. The size of the moving window was
208 based on the minimum distance that macaque troops can travel in six hours during
209 daytime (= the time interval of respective occurrence records that we had collected)
210 (Enari and Sakamaki 2011).

211 In this study, we developed models of 50 m × 50 m grid resolution following Enari
212 and Sakamaki (2011, 2012), which corresponded to the lowest resolution available in

213 the dataset for each variable (i.e., land-use pattern). Then, species occurrence maps were
214 generated for each season at the same grid resolutions, by assigning the same datasets of
215 occurrence sites described above.

216 *Analytical Procedure of ENFA*

217 ENFA is based on Hutchinson's niche concept, whereby an organism is non-
218 randomly distributed according to its ecological and physiological preferences, based on
219 existing resources in its habitat (Hirzel et al. 2002). As with the principle component
220 analysis (PCA), ENFA is able to provide insights into a species' potential habitat within
221 a given geographical context, by summarizing multiple environmental variables into a
222 few uncorrelated factors. Unlike PCA, these factors have two direct ecological
223 meanings, which allowed us to compare potential resource requirements between rural
224 and montane troops. The first meaning is related to the marginality of the species niche,
225 and indicates the deviation of mean environmental conditions from the species'
226 ecological optimum. The second meaning is related to specialisation, and is defined as
227 the narrowness of the niche relative to the global variance. The first summarized factor
228 explains all of the marginality, and part of the specialisation. The subsequent
229 summarized factors explain the remaining specialisation. Aside from obtaining scores
230 for each environmental variable, the general interpretation of ENFA yields about the
231 species niche were obtained, including global marginality and global specialisation,
232 which are calculated as root-mean-square value of each marginality (or specialisation)
233 corresponding to individual environmental variables.

234 For the ENFA procedure, we first normalized the distributions of each environmental
235 variable using the Box-Cox algorithm (Sokal and Rohlf 1981), because multinormality
236 is required for ENFA. Although ENFA is potentially robust against correlations among

237 environmental variables, because of its property, as with PCA (i.e., creating composite
238 variables) (Hirzel et al. 2002), to prevent multicollinearity and redundancy of the
239 constructed model wherever possible, we removed variables that were highly correlated
240 (i.e., correlation coefficients, >0.8) or that possessed significantly low eigenvalues, due
241 to less presence of the corresponding variable. As a result, three of the 16 variables were
242 discarded, leaving 13 variables that were assigned as inputs to the model (Table 1).
243 After summarizing the 13 variables using ENFA, we selected several significant factors
244 for further analysis using broken-stick heuristics (Hirzel et al. 2002). To calculate
245 habitat suitability, we used a median algorithm modified by Braunisch et al. (2008); in
246 brief, habitat suitability values were calculated, by assuming that on all environmental
247 factors, the median of the species distribution indicates the optimal values. Habitat
248 suitability values in each grid cell vary from 0 (unsuitable habitat) to 100 (optimum
249 habitat), and indicate how the combination of variables in a particular cell suits the
250 requirements of the subject species. The procedures were performed using Biomapper
251 Version 4.0.

252 *Evaluation of Model Predictions*

253 We evaluated the accuracy and robustness of each constructed model using a 10-fold
254 area-adjusted frequency cross-validation procedure (Fielding and Bell 1997), which
255 consists of partitioning the species dataset into 10 sets, constructing a model based on
256 nine sets, and validating the model with the remaining data set. The procedure is
257 repeated 10 times, providing the mean and variance for the validation measure. In the
258 present evaluation, the habitat suitability value was reclassified into three classes of
259 equal size: unsuitable (0–33), suitable (34–66), and optimum (67–100) macaque habitat.
260 Then, we computed the Boyce index based on the Spearman correlation coefficient

261 (Boyce et al. 2002) as a measure of model accuracy. The Boyce index varies from -1 to
262 1. Positive values close to 1 indicate high predictive value for the model (Hirzel et al.
263 2006).

264 *Habitat Unit of Rural and Montane Troops*

265 As an integrated index representing seasonal habitat quality and quantity, we
266 calculated habitat unit values for each season of rural and montane troops. The habitat
267 unit has often been regarded as an index of the carrying capacity of an area with respect
268 to the habitat resources (Giles 1978), thus providing a means of quantifying the effects
269 of habitat management. Following Schamberger and Krohn (1982), in this study, the
270 habitat unit values were defined as the product of the habitat suitability value and the
271 size of the corresponding areas (km²) of potential habitats, both of which were
272 calculated using ENFA.

273 **Results**

274 *UDs of Macaque Troops*

275 The seasonal patterns in location of UD were similar for troops S and O, which
276 differed to those of troops F and T (Fig. 2). Furthermore, the UD highlighted the
277 differences between montane and rural troops. The similarities and differences among
278 the troop UD were quantified by the overlap index. The annual mean overlap index for
279 troops S and O and troops F and T was quite high, i.e., 0.39 ± 0.11 (SD) and 0.39 ± 0.04 ,
280 respectively. In contrast, most other pairwise comparisons produced an index of less
281 than 0.1 (i.e., scarcely overlapping)— 0.04 ± 0.03 between troops S and F, 0.06 ± 0.09
282 between troops S and T, 0.07 ± 0.05 between troops O and F, and 0.10 ± 0.07 between
283 troops O and T.

284 The 95% UD areas varied with season for all four troops. In general, the values were

285 largest in spring for all UD_s (Fig. 2). The fluctuation ranges of UD size were 2.7 for
286 troop S, 2.1 for troop O, 1.4 for troop F, and 1.6 for troop T. These values indicate that
287 the UD_s of montane troops varied more with season than those of rural troops.

288 *Habitat Suitability Models*

289 In light of the highly overlapping UD_s recorded in this study, in addition to ensuring
290 sufficient input data of species occurrences, we constructed a single habitat model for
291 the montane troops and a separate one for the rural troops during each season by
292 combining the occurrence sites of troops S and O and those of troops F and T,
293 respectively. Consequently, the Boyce indices drawn from each habitat model were 0.70
294 ± 0.48 (SD) in spring, 0.95 ± 0.16 in summer, 0.70 ± 0.26 in autumn, and 0.65 ± 0.45 in
295 winter for rural troops. In comparison, these values were 0.50 ± 0.41 in spring, $1.00 \pm$
296 0.00 in summer, 0.75 ± 0.26 in autumn, and 0.95 ± 0.16 in winter for montane troops.
297 These results indicate that the accuracy of every model was high, except for the spring
298 model for montane troops, which was because of the observation sites being spatially
299 dispersed. Some of these models had rather large standard deviations around the mean
300 Boyce index because of the paucity of presence data or the occurrence of outliers within
301 the data. However, these results generally indicated that the predictive performance of
302 the habitat models was sufficiently retained, even after combining the observation sites
303 of the different troops, and for the different years.

304 As for each habitat model, we retained two to five summarized factors according to
305 the broken-stick heuristics (Table 2). The summarized factors accounted for >80% of
306 the total variance in each model and >70% of the total specialisation of the species
307 niche in all the models, except for the summer range of montane troops. In every season,
308 the value of global marginality for rural troops was higher than that of montane troops.

309 In addition, all values of global marginality for rural troop niches, except the spring
310 model, were greater than 1; this indicates that rural troops tended to only occupy areas
311 with a particular resource set, compared to the mean resource set available in the
312 reference area. In comparison, values of global specialisation demonstrated that
313 montane troops had greater environmental tolerance (i.e., wider niche breadth) than
314 rural troops. In spring, both macaque troops exhibited decreased global marginality and
315 specialisation.

316 The ENFA results for the habitat of rural troops indicate that the coefficients of factor
317 1 (i.e., marginality axis) showed relatively high negative values for the following four
318 variables in every season: mean elevation, distance to farmland, distance to road, and
319 frequency of old deciduous broadleaf forests (Table 3a). This result indicates that the
320 distributions of rural troops tended to be clumped in modified lands adjacent to human
321 settlements. The largest variance of the specialisation attributed to factor 1 in each
322 season indicates that rural troops were highly sensitive to shifts in their optimal
323 conditions; in other words, the breadth of the optimal niche for rural troops was
324 restricted to artificial rural landscapes. The other notable niche characteristic for rural
325 troops was represented by the relatively high positive coefficients for the frequency of
326 old evergreen conifer forests.

327 The results for the habitats of montane troops indicate that the coefficients of factor 1
328 (marginality axis) showed relatively high negative values for mean elevation, distance
329 to road, and distance to river or lake in every season, except spring (Table 3b). This
330 result shows that montane troops preferred lowland forests close to roads and rivers in
331 summer, autumn, and winter. In addition, the respective factors with the largest variance
332 of specialisation in summer (i.e., factor 2), autumn (i.e., factor 1), and winter (i.e., factor

333 1) showed that the niche breadth of montane troops was restricted by the elevation and
334 distance to river or lake. In comparison, the spring niche exhibited seasonally specific
335 characteristics. The troops selected mountainous areas with old deciduous broadleaf
336 forests, rarely occupying conifer forests regardless of forest age, as indicated by the
337 coefficients in factors 1 and 2.

338 *Habitat Suitability Maps*

339 We constructed seasonal habitat suitability maps from the respective sets of
340 summarized factors (Fig. 3). In all seasons, the area of optimum and suitable habitats of
341 rural troops was restricted as compared with those of montane troops. The optimum and
342 suitable habitats of montane troops were, on average, 1.75 times and 2.10 times larger,
343 respectively, than those of rural troops ($n = 4$ for both). The habitat unit values for the
344 seasonal habitats of rural troops were (in ascending order) summer (236.04) < autumn
345 (257.32) < winter (263.11) < spring (295.32), whereas those of montane troops were
346 commonly higher in every season, i.e., winter (302.00) < autumn (308.57) < summer
347 (318.07) < spring (367.01).

348 **Discussion**

349 There are two primary causes of human-macaque conflicts (Watanabe 2000; Enari
350 and Suzuki 2010; Muroyama and Yamada 2010). The first is the decrease in the
351 carrying capacity of montane areas for macaques, which is caused by past artificial
352 habitat manipulation. The second is the increase in the carrying capacity of rural areas,
353 which originates from the decline of human activities due to recent rapid human
354 depopulation in rural Japan (Tsunoda and Enari 2012). Hence, to obtain an ideal balance
355 between the conservation of vulnerable macaque populations, while simultaneously
356 preventing them from causing damage, it is necessary to increase the habitat unit of

357 montane troops and decrease that of rural troops. As distinct differences in seasonal
358 resource uses between montane and rural troops were detected (Table 3), this objective
359 could be achieved.

360 *Priority Conservation Areas for Montane Macaque Habitats*

361 Along with the spatial patterns of UDs (Fig. 2), environmental factors influencing
362 the potential habitat of montane troops varied widely with respect to season, compared
363 to rural troops (Table 3b). This indicates that the seasonality of resource use should not
364 be disregarded when exploring potential conservation strategies.

365 In spring, montane troops migrated to areas of higher elevation (Fig. 2, Table 3b).
366 This observation does not support previous studies (Izumiyama 2002; Koganezawa
367 2002), which found that seasonal vertical-migration to higher-elevation areas occurred
368 in summer, due to the distribution patterns of their staple foods (Hanya 2010). To
369 examine the ecological causes for this seasonal discrepancy (i.e., spring versus summer),
370 more information about the factors that influence migration is required. However, this
371 difference may be partly explained by the high positive coefficient values of the spring
372 marginality axis for montane troops, especially with respect to old broadleaf forests (i.e.,
373 primary beech forests) (Table 3b). The leaves of beech trees serve as a staple food for
374 macaques during spring in the study area (Enari 2007), with these primary forests
375 having only been intensively preserved in areas of relatively high elevation. In addition,
376 given the fact that optimum or suitable habitats were solely concentrated in those areas
377 (Fig. 3), the conservation priority for the spring habitat of montane troops should be
378 directed toward intact forest areas that were originally distributed in the cool-temperate
379 zone, namely the World Natural Heritage sites.

380 However, primary forests were rarely occupied by any of the macaque troops, except

381 during spring. This observation logically implies that primary forests do not always
382 function as high-quality habitat for macaques. This may be due to the climax forests of
383 cool-temperate forests being primarily composed of beech trees with poor understory
384 vegetation, resulting in a uniform forest with low plant diversity. In fact, Sakamaki et al.
385 (2011) empirically demonstrated that the biomass and diversity of dietary resources
386 preferred by macaques (i.e., shade-intolerant trees) are lower in primary beech forests
387 than conifer plantations during winter.

388 From summer to winter, the resource use of montane troops was not clearly affiliated
389 (i.e., no positive selectivity) to any forest cover type. In comparison, the relative
390 importance of environmental factors with respect to geographical features increased
391 across the seasons. In particular, as shown in the marginality axis, the distribution of
392 suitable habitats for montane troops was biased toward lowland areas adjacent to rivers
393 or roads, i.e., the geographical space with forest edge effects. A similar phenomenon has
394 been observed in other cool-temperate forests. For example, Imaki et al. (2006)
395 demonstrated that such biased habitat occupation might be explained in terms of the
396 abundance of dietary resources. Hence, it may be reasonable to propose that the habitat
397 unit for montane troops is effectively enhanced (in contrast to that of rural troops) by
398 removing old plantations of evergreen conifers (i.e., abandoned commercial-forests,
399 mainly composed of closed- canopy forests of *C. japonica* and *C. obtuse*) from the
400 forest edge at low elevations. This is because there was an obvious discrepancy in the
401 selectivity of montane troops (i.e., negative selectivity) to plantations, in comparison to
402 that of rural troops (i.e., positive selectivity) (Table 3). Given that conifer plantations
403 are commonly harvested before turning into old plantation under standard forestry
404 operation, this suggestion logically implies that the appropriate plantation management

405 in forest edges does not necessarily contradict the habitat conservation initiatives for
406 montane troops.

407 ***Priority Management Areas for Rural Macaque Habitats***

408 In contrast to the potential habitat of montane troops, rural troops were more biased
409 in their resource use and had narrower niche breadths, which were represented by high
410 values of both global marginality and specialisation, respectively, throughout the year
411 (Table 2). Specifically, rural troops consistently occupied habitats that depend on
412 artificially developed rural environments. This preference was not only visually
413 demonstrated in the uniform spatial distribution of UDs (Fig. 2), but was also quantified
414 by the coefficients of the marginality axis (Table 3a). These obvious discrepancies in
415 habitat properties compared with montane troops might be recognized as favourable
416 consequences toward focusing actual management plans by specifying priority areas to
417 reduce or prevent damage caused by rural troops.

418 Based on the objective to reduce the habitat unit of rural troops effectively, it should
419 be noted that the winter habitats of macaques showed the second highest habitat unit
420 values, even though winter is a typical bottleneck season for wild macaques, due to
421 severe food shortages (Tsuji 2010). Usually, the total calorific intake available from
422 natural winter foods is below the basal metabolic rate of macaques in cool-temperate
423 forests (Nakayama et al. 1999). Hence, our finding for rural troops is unexpected, and
424 might be explained by the fact that farmlands function as resting and feeding sites for
425 these macaques, even in winter. This is because farmlands are usually located in sunny,
426 non-windy lowland areas, with the levels of farming activity during the agricultural off-
427 season being low. According to a previous observation study (Enari 2007), rural
428 macaques spend most of their time in apple orchards during winter, feeding on buds and

429 bark, or digging up fallen apples buried beneath the snow cover. This extremely
430 specialized winter habitat is quantitatively corroborated by the high global specialisation
431 values that were obtained for this niche during this study. These results suggest the
432 possibility that intensive prevention against macaque intrusions to settlements during
433 the bottleneck snowy seasons (e.g., by not removing macaque-proof fences even during
434 agricultural off-seasons)—to which little attention has been directed—might contribute
435 substantially toward reducing the habitat unit of rural troops, and in turn directly affect
436 population density.

437 Rural troops exhibit other notable habitat characteristics. In contrast to montane
438 troops, rural troops positively occupied old evergreen conifer forests. This forest cover
439 usually provides limited attractive food resources to macaques (Hanya 2010). However,
440 this habitat may function as a protective environment, concealing macaques from
441 humans, as demonstrated by Imaki et al. (2000, 2006). Given that these environments,
442 which are distributed around human settlements, may serve as a front-line refuge for
443 rural troops intruding into farmlands, we may reasonably conclude that the landscape
444 mosaic composed of old plantations and farmlands should be preferentially removed to
445 improve the regulation of rural troop habitat units.

446 ***Future tasks***

447 Resource uses by Japanese macaques are also sensitive to annually fluctuating
448 environmental factors, such as nut fruiting levels (Tsuji et al. 2006; Tsuji and Takatsuki
449 2009); the frequency and strength of cold weather fronts (Watanuki and Nakayama
450 2003); and the occurrence of arbitrary natural disasters, such as typhoons (Tsuji and
451 Takatsuki 2008). For example, montane troops in the Shirakami Mountains have been
452 observed to move their winter range to areas of lower elevation and to shift their diets

453 from the bark and buds of shrub trees to those of arboreal trees, when subjected to
454 irregular and prolonged bouts of heavy snow (Enari and Sakamaki-Enari in press).
455 While the generality of the current habitat models could be fairly retained under normal
456 environmental conditions, their robustness would be enhanced by integrating stochastic
457 environmental fluctuations, thus contributing additional dimensions in the drafting of
458 medium- and long-term habitat management plans.
459

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470

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Figure legends

Fig 1 Land cover (a) and panoramic view (b) of reference area, located in the northeastern Shirakami Mountains, northernmost mainland area of Japan

Fig 2 Seasonal utilization distributions (UDs) of Japanese macaque troops in the Shirakami Mountains between 2008 and 2009, estimated by the fixed kernel method. Values in parentheses represent the number of occurrence sites used in the kernel method, and the number of days spent collecting the occurrence sites through the radio-tracking work. Black- coloured areas = 95% UD, the size of which were shown in each box; areas surrounded by dashed lines = reference area; grey line and grey coloured areas = river or lake

Fig 3 Seasonal habitat suitability maps for rural and montane troops of Japanese macaques in the Shirakami Mountains between 2008 and 2009. The habitat suitability values are provided in parentheses

Table 1 Environmental variables included in ecological-niche factor analysis for Japanese macaque habitats

Category	Global			Application for
Environmental variable	mean	Range	SD	a final model
Topography				
Mean elevation (m)	356.8	79.5–871.6	148.4	yes
Mean Slope (°)	21.6	0.0–50.0	9.6	yes
SD of elevation (i.e., undulation of land surface)	54.0	3.6–135.7	22.9	yes
^a Frequency of northern slope	0.3	0.0–0.9	0.1	yes
^a Frequency of southern slope	0.2	0.0–0.8	0.1	yes
Land use				
Distance to farmland (km)	3.2	0.0–9.6	2.9	yes
^a Frequency of abandoned farmland	0.0	0.0–0.4	0.0	no
Distance to dwelling land (km)	3.7	0.0–10.0	2.9	no
Distance to road (km)	0.7	0.0–3.5	0.7	yes
Hydrology				
Distance to river or lake (km)	0.3	0.0–1.4	0.2	yes
Forest cover				
^a Frequency of old deciduous broadleaf forests	0.2	0.0–1.0	0.3	yes
^a Frequency of young deciduous broadleaf forests	0.4	0.0–1.0	0.3	yes
^a Frequency of old deciduous conifer forests	0.0	0.0–0.5	0.1	yes
^a Frequency of young deciduous conifer forests	0.0	0.0–0.0	0.0	no
^a Frequency of old evergreen conifer forests	0.1	0.0–0.7	0.1	yes
^a Frequency of young evergreen conifer forests	0.2	0.0–1.0	0.2	yes

^aThese variables were originally composed of Boolean values. Hence, we provided continuous values by using the moving window technique.

Table 2 Global marginality and specialisation values for rural and montane troops of Japanese macaques in the Shirakami Mountains. The values were extracted from the summarized factors used in the final model. The number of the summarized factors according to broken-stick heuristics is shown in parentheses

	Rural troops				Montane troops			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
	(3)	(3)	(4)	(3)	(5)	(3)	(2)	(4)
Global marginality ^a	0.91	1.22	1.15	1.19	0.52	0.74	0.89	0.91
Global specialisation ^b	2.40	4.12	3.01	17.56	1.56	1.88	3.03	2.56
Variance explained (%)	89.2	94.4	93.1	99.7	86.9	83.2	88.0	89.7
Specialisation explained (%)	78.5	88.9	86.2	99.4	73.8	66.4	75.9	79.5

^aAs the value increases, species distribution becomes more biased with respect to the mean available environmental conditions in the reference area.

^bAs the value increases, the width of the species' niche decreases.

Table 3 Variance explained by the first two summarized factors (F1 and F2) expressed as coefficient values for each variable in rural troops (a) and montane troops (b). Coefficients of F1 (marginality factor) range from -1 to $+1$ for each variable: positive values represent positive selection, whereas negative values represent negative selection relative to the mean conditions in the reference area. Specialisation coefficients range from -1 to $+1$: a higher absolute value of the coefficient represents a more restricted range of the macaques on the corresponding variable. The amount of specialisation in each factor is given between parentheses

(a) Seasonal habitats of rural troops

Variables	Spring		Summer		Autumn		Winter	
	F1	F2	F1	F2	F1	F2	F1	F2
	(56.8)	(15.8)	(69.5)	(14.0)	(60.6)	(13.4)	(98.6)	(1.0)
Mean elevation	-0.37	-0.18	-0.51	-0.24	-0.41	-0.24	-0.46	0.16
Mean slope	0.04	-0.07	-0.10	0.07	-0.06	-0.14	-0.06	-0.06
SD of elevation	-0.06	-0.20	-0.17	-0.07	-0.15	-0.12	-0.13	0.07
Frequency of northern slope	0.18	-0.02	0.23	0.02	0.38	-0.01	0.31	-0.02
Frequency of southern slope	-0.20	0.00	-0.05	0.09	-0.26	0.00	-0.15	-0.02
Distance to farmland	-0.62	0.54	-0.60	-0.27	-0.58	0.58	-0.60	0.33
Distance to road	-0.32	0.05	-0.35	-0.01	-0.25	0.03	-0.33	-0.02
Distance to river or lake	-0.15	0.02	-0.13	0.06	-0.14	0.07	-0.12	-0.04
Frequency of old deciduous broadleaf forests	-0.38	-0.78	-0.31	0.91	-0.33	-0.73	-0.33	-0.90
Frequency of young deciduous broadleaf forests	0.08	0.13	-0.14	0.13	-0.02	0.17	0.02	-0.18
Frequency of old deciduous conifer forests	-0.02	0.00	-0.09	-0.07	-0.09	-0.10	-0.07	-0.02
Frequency of old evergreen conifer forests	0.34	-0.10	0.17	0.07	0.24	-0.06	0.24	-0.12
Frequency of young evergreen conifer forests	0.11	0.02	0.01	0.05	-0.02	0.02	-0.04	-0.03

(b) Seasonal habitats of montane troops

Variables	Spring		Summer		Autumn		Winter	
	F1	F2	F1	F2	F1	F2	F1	F2
	(20.6)	(25.0)	(8.6)	(35.9)	(60.3)	(15.6)	(46.9)	(17.0)
Mean elevation	-0.04	0.18	-0.44	-0.62	-0.45	0.47	-0.47	0.56
Mean slope	0.20	-0.02	-0.29	-0.02	-0.04	-0.04	-0.13	-0.10
SD of elevation	0.25	0.02	-0.27	-0.03	0.02	-0.21	-0.09	-0.13
Frequency of northern slope	-0.16	0.02	0.02	0.04	-0.26	0.07	-0.21	0.21
Frequency of southern slope	0.06	-0.16	0.06	0.07	0.14	0.13	0.13	0.21
Distance to farmland	0.66	0.51	0.40	-0.58	-0.14	-0.20	-0.08	-0.28
Distance to road	-0.11	-0.06	-0.48	0.08	-0.56	0.24	-0.55	0.10
Distance to river or lake	0.11	-0.23	-0.40	0.23	-0.41	-0.12	-0.45	-0.11
Frequency of old deciduous broadleaf forests	0.29	0.09	-0.10	0.20	-0.41	-0.74	-0.39	-0.62
Frequency of young deciduous broadleaf forests	0.06	0.03	0.01	0.11	0.09	-0.01	0.04	0.15
Frequency of old deciduous conifer forests	-0.34	0.77	-0.26	-0.39	0.03	-0.05	-0.07	-0.16
Frequency of old evergreen conifer forests	-0.31	0.09	-0.12	0.11	-0.18	0.11	-0.16	0.01
Frequency of young evergreen conifer forests	-0.33	0.14	0.06	0.03	-0.01	0.20	-0.06	0.20

Fig. 1

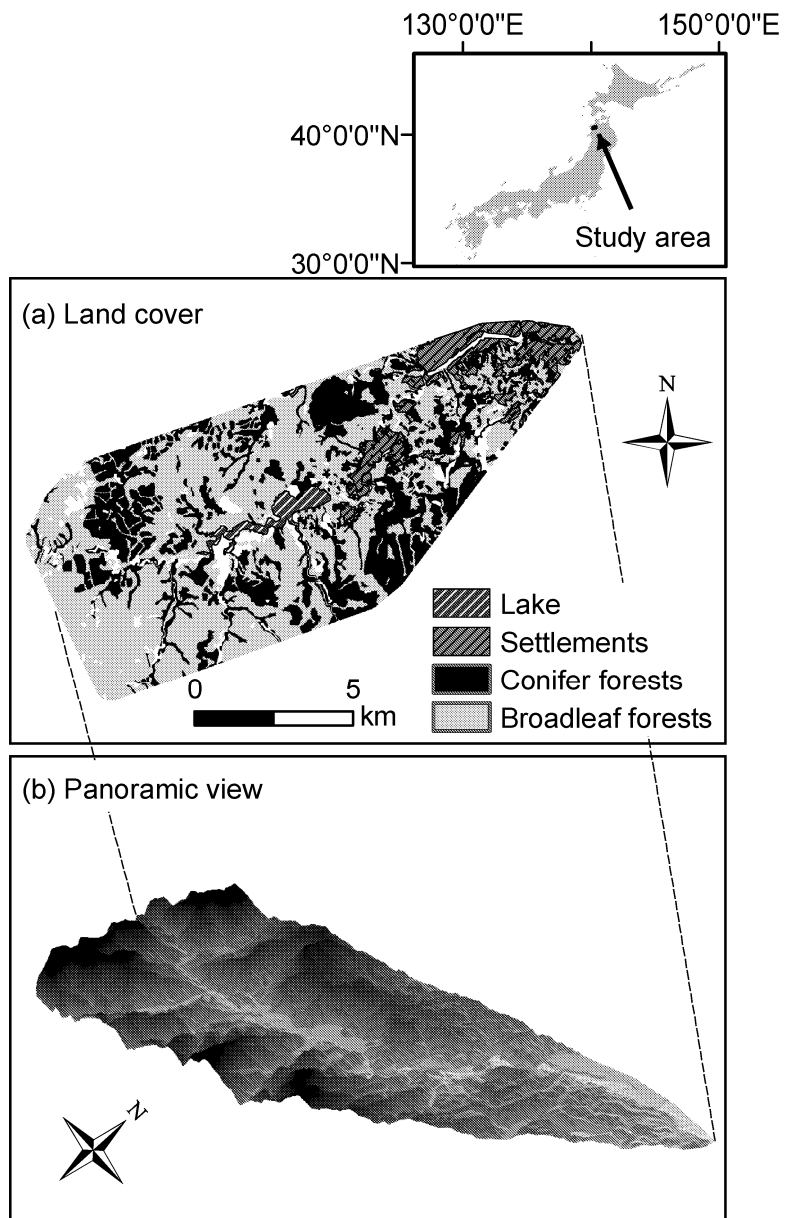


Fig. 2

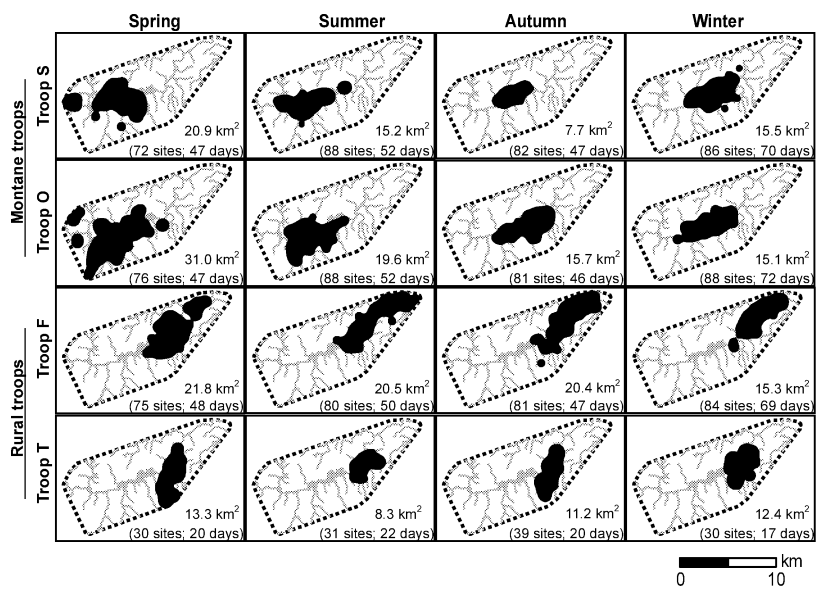


Fig. 3

