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Authors: Suzuki, Mio, and Saito, Masayuki U.

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RESEARCH PAPER

Seasonal changes in forest road use by mammals in a heavy snowfall area, north-eastern Japan: effects of management intensities

Mio SUZUKI[1] and Masayuki U. SAITO[2*]

[1] *Graduate School of Agricultural Sciences, Yamagata University, Tsuruoka, Japan; e-mail: suzu7yy@gmail.com*

[2] *Faculty of Agriculture, Yamagata University, Tsuruoka, Japan; e-mail: saito.ume@gmail.com*

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Abstract. Forest road use by mammals can vary in response to both the management intensity of the forest roads and the seasonal changes in their environments. We investigated the effects of seasonal changes in heavy snowfall areas on road use by mammals in forest environments with different management intensities. The field survey was conducted in north-eastern Japan from August 2022 to July 2023. Using camera traps, we observed the frequency of occurrence of each species on forest roads, decommissioned roads, and forest interior sites. We employed a generalized linear mixed model to analyse the relationship between the occurrence events of each species and site types and seasons. Red foxes occurred significantly more frequently on forest roads than in forest interiors during all seasons. Raccoon dogs selectively used forest roads in spring and winter. However, Japanese martens, Japanese hares, and wild boar only occasionally occurred on forest roads. These findings suggest that selectivity in the use of forest roads varies among species, and selectivity for forest roads and decommissioned roads varies seasonally.

Key words: carnivore, camera trap, decommissioned road, forestry, forest management, road ecology

Introduction

Anthropogenic disturbances to the natural environment significantly impact ecosystems, resulting in biodiversity loss (Maxwell et al. 2016). Given the inherent challenges in restoring human-disturbed environments, assessing the effects of such disturbances on wildlife is important. Intensive forestry and forest management play an important role in anthropogenic disturbance by significantly altering natural habitats and influencing wildlife ecology and behaviour (Demarais et al. 2017). Changes in wildlife ecology and behaviour, in turn, can profoundly affect the structure and function of forest ecosystems. Therefore, understanding the impacts of forestry and forest management on ecosystems is essential for promoting the coexistence of people and nature.

The construction of forest roads is a common practice in forestry and forest management. These forest roads often contribute to the degradation of wildlife habitats (Lambert et al. 2014). However, despite their potential negative impacts, forest roads are characterized by low barrier effects (Chen & Koprowski 2019) and are not insurmountable structures (Saklaurs & Baltmanis 2014), suggesting that they may have relatively weak negative impacts on wildlife. Some mammals use forest roads as foraging sites (e.g. Yakushika *Cervus nippon yakushimae*: Terada et al. 2010) or movement

* *Corresponding Author*

routes (e.g. wolf *Canis lupus*: Eriksen et al. 2009, Zimmermann et al. 2014, St-Pierre et al. 2022; red fox *Vulpes vulpes* and raccoon dog *Nyctereutes procyonoides*: Suzuki & Saito 2023, Suzuki et al. 2023). In addition, frequent road use may increase encounters with conspecifics and other species that similarly use roads (Roever et al. 2008), thereby creating conditions for increased population size, spread of infectious disease, and increased intra- and interspecific competition (Hill et al. 2021). The use of roads as movement routes for mammals can also affect the range expansion of both native and non-native species (Huey 1941), leading to increased opportunities for human-wildlife encounters as animals follow roads into human-inhabited areas. Compared to paved roads, forest roads are more easily traversed by mammals, contributing to a variety of impacts on ecosystems and human society.

The environment of forest roads varies depending on the intensity of management. Some forest roads are continuously managed for human movement within the forest. In contrast, others, such as temporary roads like forest work roads in Japan, are managed for short periods to facilitate logging activities (Ministry of Agriculture, Forestry and Fisheries 2023). In cases where a forest road is no longer actively managed, the invasion of pioneer plants over a short period results in dense growth of understory vegetation and shrubs, rendering the road inaccessible to general vehicles (here referred to as a 'decommissioned road'). Differences in forest road environments influence road use by mammals. For example, forest roads with little understory vegetation are more frequently used by mammals because they are easier to walk on (Di Bitetti et al. 2014), whereas mammals less frequently use decommissioned roads with dense understory vegetation (Suzuki & Saito 2023). However, the forest road environment in the cool temperate zone undergoes significant seasonal changes. Winter snowfall causes the understory vegetation to flatten, potentially making even decommissioned roads easier to walk (i.e. reducing movement costs), thus leading to a resumption of mammalian use. Despite the seasonal variation in forest road environments, current assessments of mammalian road use do not adequately account for these changes. By focusing on regions with heavy snowfall and substantial seasonal environmental variation, we expect to gain a more comprehensive understanding of the seasonal effects on mammalian road use.

In this study, we investigated the effects of seasonal changes in heavy snowfall areas on road use by mammals in forest environments with different management intensities. We formulated two hypotheses: 1) during the non-snowy season (i.e. spring, summer, and autumn), animals preferentially use forest roads due to the absence of understory vegetation, making them more accessible compared to decommissioned roads or forest interior, and 2) during the snowy season (i.e. winter), animals use forest roads and decommissioned roads equally because the snow cover creates a uniform understory environment. To test these hypotheses, we examined the seasonal frequency of occurrence of mammals on forest roads, decommissioned roads, and forest interior.

Material and Methods

Survey area

This study was conducted in the Nishiaraya area, Tsuruoka City, Yamagaga Prefecture, north-eastern Japan (38°38′ N, 139°49′ E, Fig. 1). The study area is located in the cool temperate zone, with an average annual temperature of 12.9 °C and annual precipitation of 2,191.4 mm from 1991 to 2020 (Japan Meteorological Agency 2020). The forests in the study area are predominantly composed of artificially planted evergreen coniferous cedar (*Cryptomeria japonica*), with other deciduous broad-leaved trees

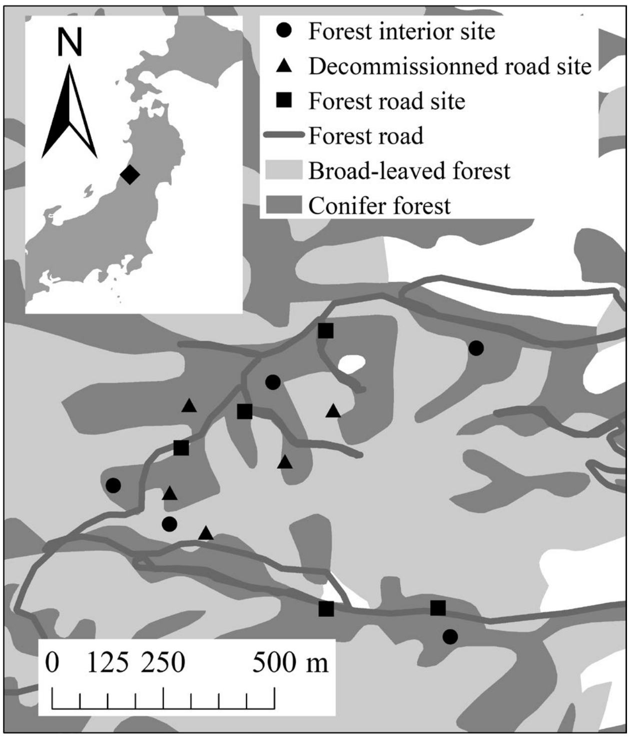

Fig. 1. Location of the study area. Broad-leaved and coniferous forests were extracted based on the legend of the 1:25,000 vegetation map by the Ministry of the Environment (Biodiversity Center of Japan 2012).

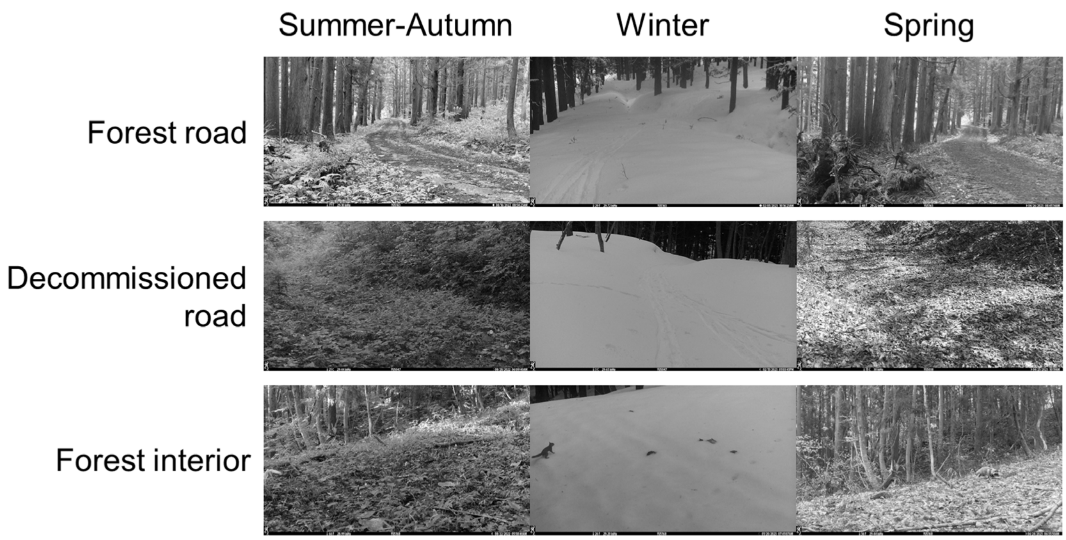

Fig. 2. Examples of seasonal changes in camera trap sites on a forest road, a decommissioned road, and a forest interior. Seasonal changes for each site type are shown for the same camera trap site.

such as Japanese beech (*Fagus crenata*) and Japanese oak (*Quercus crispula*) also present.

For the field survey, we selected forest roads and decommissioned roads within the study area (Fig. 2). The forest road used for the survey was unpaved, approximately two meters wide, and accessible to vehicular traffic with minimal vegetation on the road surface. The decommissioned road used for the survey was also unpaved approximately two meters wide but was no longer open to vehicular traffic due to dense understory vegetation and shrubs. This decommissioned road had previously served as a forest working road, and its slope was slightly steeper than the forest road (Fig. S1). In winter, forest roads, decommissioned roads, and all forest areas were covered with a snow depth of 100-200 cm, and the understory vegetation was almost absent above the snow. While there was vehicle traffic on forest roads during the non-winter season, there was limited use of snow vehicles, snowmobiles, or human activity during the winter season.

Camera trapping survey

We conducted a camera trapping survey from August 2022 to July 2023 to assess the use of forest roads and decommissioned roads by mammals. For this survey, we designated fifteen sites, comprising five forest road sites, five decommissioned road sites, and five forest interior sites (Figs. 1, 2). The forest interior sites were located within the forest, with an effort to maintain a vertical distance of 50 m from the forest road (Di Bitetti et al. 2014, Suzuki & Saito 2023, Suzuki et al. 2023). At each site, we installed a sensor camera (Dark Ops Apex, Browning, Alabama, USA) at a height of 80 cm. During winter, we visited the camera sites every week or two to adjust the height and angle of view and to ensure that snow accumulation did not alter the coverage (Suzuki et al. 2023). In other seasons, we checked each camera once a month. The camera was configured to capture five consecutive photographs per detection, with a one-minute interval between detections. We used the captured photographs for species identification. To avoid duplicate photographs of the same individual, individuals of the same species captured within 30 minutes at the same site were treated as a single occurrence event (O'Brien et al. 2003).

Data analysis

To examine the relationship between the number of occurrence events of each species captured in camera traps and the factors of season and site type (forest road, decommissioned road, forest interior), we constructed a generalized linear mixed model (GLMM). Given the persistence of shrub branches after defoliation and the substantial environmental changes following snow accumulation, we categorized seasons into three groups: 'summer-autumn' from July to November, characterized by thriving understory vegetation; 'winter' from January to March and December, characterized by snow accumulation; and 'spring' from April to June, with occurs before snowmelt and when understory vegetation flourishes (Fig. 2). The response variable was the number of occurrence events of each mammal species recorded each month at each site. To assess the influence of each site type, taking into account seasonal effects, we used season and a site type-season interaction term as explanatory variables. The number of occurrence events of mammals was assumed to follow a Poisson distribution with a log link function. The logarithm of camera days was

Table 1. The number of occurrence events of each mammal in the study area. This value was calculated by treating individuals of the same species photographed within 30 min at the same site as a single event. Japanese martens, red foxes, raccoon dogs, wild boar and Japanese hares, which occurred more frequently, were used for subsequent generalized linear mixed model (GLMM) analysis.

Species	Scientific name	No. of occurrence events			
		Forest roads	Decommissioned roads	Forest interior	Total
Japanese marten	*Martes melampus*	133	92	117	342
Red fox	*Vulpes vulpes*	247	53	21	321
Raccoon dog	*Nyctereutes procyonoides*	146	83	36	265
Wild boar	*Sus scrofa*	56	94	62	212
Japanese hare	*Lepus brachyurus*	57	89	61	207
Japanese squirrel	*Sciurus lis*	70	22	33	125
Asian black bear	*Ursus thibetanus*	47	15	17	79
Japanese serow	*Capricornis crispus*	8	10	21	39
Masked palm civet	*Paguma larvata*	16	11	9	36
Japanese badger	*Meles anakuma*	13	16	0	29
Japanese macaque	*Macaca fuscata*	5	5	13	23
Japanese weasel	*Mustela itatsi*	3	8	6	17
Sika deer	*Cervus nippon*	6	1	4	11
Camera days		1,609	1,595	1,669	4,873

included in the offset term to account for potential variation in the camera trap duration by month and site. Random intercepts for sites were included to address site-to-site variability. The percentage of deviance explained (%DE) was used to indicate the explanatory power of each model.

As a preliminary analysis, we checked the spatial autocorrelation of our data because spatial autocorrelation can lead to misleading parameter estimates (Dormann et al. 2007). We performed Moran's *I* correlograms using the residuals from the GLMM for each species. Because all Moran's *I* for lag distances (50-600 m) in each GLMM were low ($|I| < 0.1$, $P \geq 0.05$), we assumed that there was no spatial autocorrelation (e.g. Saito & Koike 2013).

The analysis was conducted using R version 4.2.2 (R Core Team 2022), using the glmmTMB function from the 'glmmTMB' package, the moran function from the 'spdep' package, and the ggpredict function from the 'ggeffects' package.

Results

Camera-trapping survey

We identified a total of 13 mammal species (forest road: 13 species, decommissioned road: 13 species, forest interior: 12 species) over 4,873 camera days (forest road site: 1,609 days, decommissioned road site: 1,595 days, forest interior site: 1,669 days) through camera trap surveys. The detected species included Japanese martens (*Martes melampus*), red foxes, raccoon dogs, wild boar (*Sus scrofa*), Japanese hares (*Lepus brachyurus*), Japanese squirrels (*Sciurus lis*), Asian black bears (*Ursus thibetanus*), Japanese serows (*Capricornis crispus*), masked palm civets (*Paguma larvata*), Japanese badgers (*Meles anakuma*), Japanese macaques (*Macaca fuscata*), Japanese weasels (*Mustela itatsi*), and sika deer (*Cervus nippon*) (Table 1). Our analysis focused on five species frequently captured in photographs: Japanese marten, red fox, raccoon dog, wild boar, and Japanese hare.

Relationships between the occurrence events and site types and seasons

The GLMM results showed that the responses of species to site types varied among seasons (Fig. 3, Table S1). For Japanese martens, there were no significant differences in the number of occurrence events between forest roads and decommissioned roads, as well as between forest roads and forest interiors in each season ($P \geq 0.05$; Fig. 3). Red foxes were significantly more likely to occur on forest roads than on decommissioned roads or in forest interiors during summer-autumn and spring ($P < 0.05$; Fig. 3),

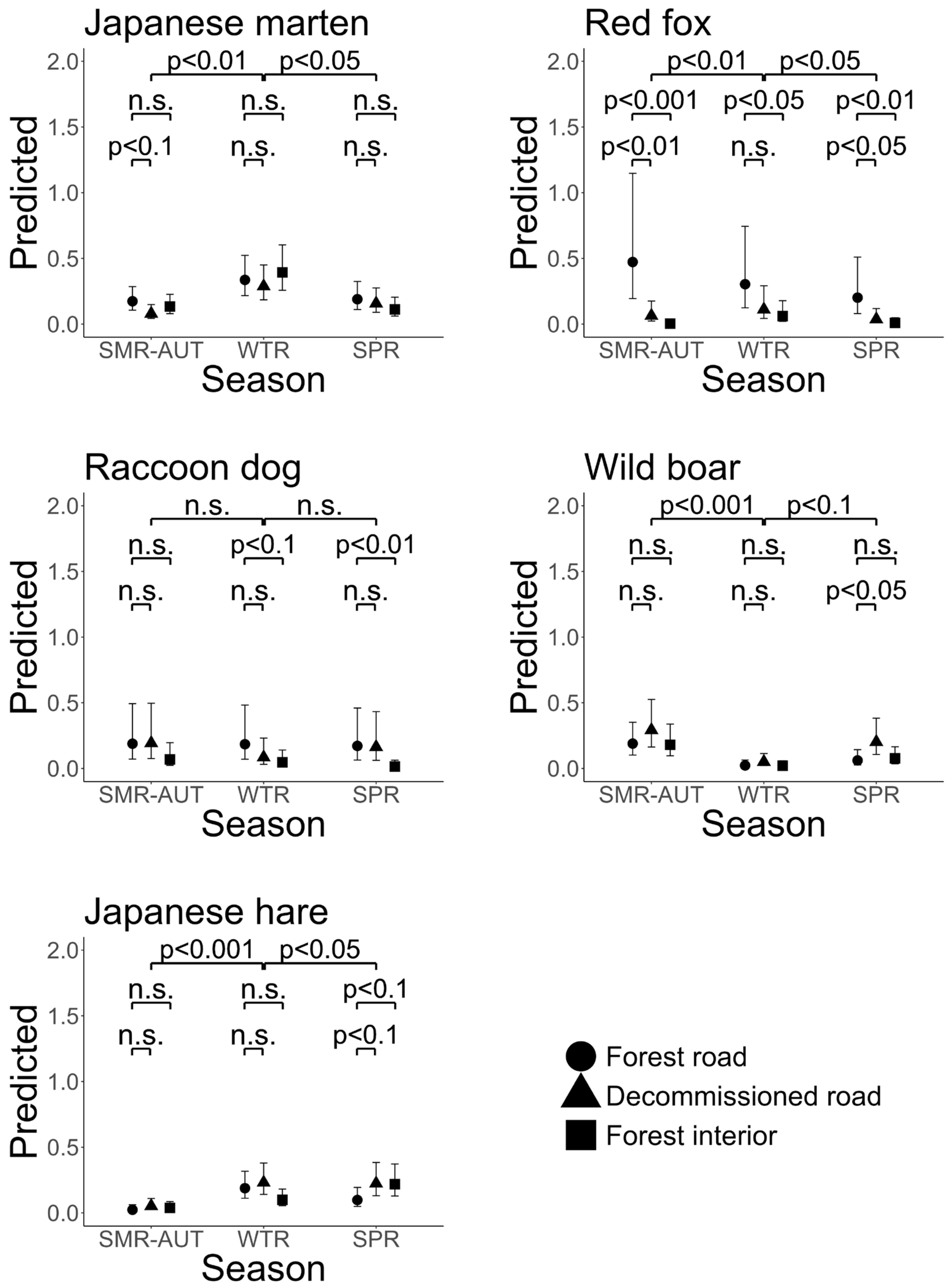

Fig. 3. The results of generalized linear models (GLMMs) for Japanese martens, red foxes, raccoon dogs, wild boar, and Japanese hares. The vertical axis represents the predictions in each model obtained using the ggpredict function of the R package 'ggeffects'. Error bars represent 95% confidence intervals. Detailed parameter estimates in each GLMM are shown in Table S1.

and significantly more likely to occur on forest roads than in forest interiors during winter ($P < 0.05$; Fig. 3). Raccoon dogs were significantly more frequent occur on forest roads than in the forest interior in spring ($P < 0.01$; Fig. 3), and a similar trend was observed in winter ($P < 0.1$; Fig. 3), although no significant differences were found. Wild boar occurred significantly more often on decommissioned roads than on forest roads in spring ($P < 0.05$; Fig. 3). Japanese hares tended to occur more frequently on decommissioned roads and in forest interior than on forest roads in spring ($P < 0.1$; Fig. 3), although no significant differences were detected.

The %DE of the GLMMs for Japanese martens, red foxes, raccoon dogs, wild boar, and Japanese hares were 18.2%, 49.3%, 24.8%, 21.7%, and 21.1%, respectively (Table S1).

Discussion

Red foxes exhibited the highest %DE in the GLMM and occurred significantly more frequently on forest roads than in the forest interior in all seasons (Fig. 3). However, differences in occurrence between forest roads and decommissioned roads for red foxes varied by season, with no significant differences detected only in winter. This finding suggests that, although the high selectivity for forest roads by red foxes remains unchanged during the snowy season, their relative importance may decrease. These findings support the hypotheses that 1) during the non-snow season, animals use forest roads more than decommissioned roads or forest interiors, and 2) during the snow season, animals use forest roads and decommissioned roads equally. For raccoon dogs, there was a weak tendency to selectively use forest roads only in spring and winter (Fig. 3), partially supporting the hypothesis. In contrast, the hypotheses were not supported for Japanese martens, Japanese hares, and wild boar, as these species tended to occur infrequently on forest roads. These results suggest that selectivity to forest roads varies among species. However, in all species, selectivity for forest roads and decommissioned roads varied seasonally (Fig. 3), suggesting that seasonal environmental changes on each road also influence mammalian behaviour.

Medium-sized carnivores

Carnivora is the mammalian order with the largest number of road-using species (Hill et al. 2021), and they also selectively use forest roads (Suzuki & Saito 2023). In this study, however, seasonal changes in forest road selectivity in red foxes, raccoon dogs, and Japanese martens varied with species (Fig. 3). The differences among these three species can be attributed to the different purposes of forest road use.

Red foxes had the highest selectivity for forest roads among the three species, possibly because red foxes use forest roads as movement routes (Suzuki et al. 2023). Many canids walk routes with lower travel costs to reduce physical exertion and improve prey detection and capture rates by searching a larger area (e.g. coyotes *Canis latrans*: Gese et al. 2013, wolves: Droghini & Boutin 2018). In our study area, red foxes are known to frequently forage small mammals (Nakane et al. 2022, Enomoto et al. 2023), supporting the idea that they selectively choose to use forest roads. The observed reduction in the forest road use by red foxes only during winter may be due to snow cover burying the understory vegetation on decommissioned roads, creating an environment with movement costs nearly equivalent to those on forest roads. Many decommissioned roads in the study area were formerly working roads with slightly steeper slopes. If a similar comparison were made with gently sloping decommissioned roads, it is possible that red foxes would use these roads in winter to the same extent as forest roads.

The reason that raccoon dogs were less likely to actively use forest roads than red foxes (Fig. 3) may be that, given the characteristics of raccoon dogs' winter diet (Sasaki & Kawabara 1994, Enomoto et al. 2018, Kumagai & Saito 2022), they do not hunt as much as red foxes (Baltrūnaitė 2006, Sutor et al. 2010, Drygala et al. 2014) and do not need to be as specific about their movement routes. Seki & Koganezawa (2011) suggested that raccoon dogs reduce activity and minimize energy expenditure in cool temperatures and deep snow, which may lead to their selective use of forest roads due to increased movement costs associated with snow cover in the study area. Because understory vegetation tends to thrive earlier in the spring along forest roads than in the forest interior (Ng et al. 2008), raccoon dogs may use forest roads to increase the accessibility of their primary food resources, such as fruits and insects. The lack of selectivity for forest roads in raccoon dogs during summer-autumn may be due to the proximity of settlements and gentler slopes in our study area compared to Suzuki & Saito (2023). Variations in movement routes and foraging habitat potential in response to seasonal and environmental changes may alter the selectivity of forest roads in raccoon dogs.

The non-selectivity of forest roads in Japanese martens (Fig. 3) may be due to their high tree-climbing ability (Okawara 2018) and low concern for travel costs. Previous studies have shown that genus *Martes* are less likely to use forest roads (e.g. Iannarilli et al. 2021), and this study is generally consistent with those findings. However, Suzuki et al. (2023) suggested that Japanese martens use forest roads in winter to minimize movement costs in years with high snowfall. It is possible that Japanese martens did not actively use forest roads in this study due to the somewhat low snowfall year during the observation period.

Japanese hares

Japanese hares did not exhibit a tendency to use forest roads in all seasons selectively and tended to avoid forest roads in spring ($P < 0.1$; Fig. 3). This finding is consistent with a previous study conducted under snowy winter conditions (Suzuki et al. 2023). Habitat selection during the active hours of Japanese hares prioritizes foraging over predator avoidance (Suzuki et al., unpublished data). Because Japanese hares feed on shrubs that emerge from snowmelt, they may preferentially use decommissioned roads and forest interiors, which tend to have more shrubs than forest roads, during the spring. Japanese hares, which are herbivores, may use forest roads depending on the condition of their food plants.

Wild boars

Wild boar exhibited selective use of decommissioned roads rather than forest roads during the spring (Fig. 3). This result is consistent with previous studies indicating that large mammals preferentially use forest working roads and decommissioned roads (Lacerte et al. 2022, St-Pierre et al. 2022, Scalbert et al. 2023). Forest roads are known to be foraging areas for large mammals (Terada et al. 2010, Keken et al. 2019), and wild boar, in particular, are involved in digging vegetation along roads to forage for earthworms and insect larvae (Groot Bruinderink & Hazebroek 1996). However, because wild boar are game animals and tend to avoid human activities (Saito et al. 2011, 2012, van Doormaal et al. 2015), they may be cautious about using forest roads. Nevertheless, the observation that wild boar preferred decommissioned roads with low human activity in spring may be due to the need to replenish their nutritional resources after the severe winter conditions, as winter snow cover provides a challenging environment for wild boar. Seasonal changes in the trade-off between benefits and costs may account for the seasonal variation in the use of decommissioned roads by wild boar.

Conclusions

This study assessed the seasonal use of forest roads by mammals in relation to the management intensity of these roads, suggesting that certain mammals selectively use forest roads in response to environmental changes. The forest road environment would influence the behaviour of mammals using these roads, highlighting the importance of environmental factors in understanding road use by mammals. However, the season and purpose of forest road use varied among species. The results of this study suggest that forest road management can contribute to the conservation and management of specific mammal groups. For example, appropriate forest roads may improve the quality of threatened carnivorous habitats. Our findings on wild boar habitat use may also apply to population management. Our results also suggest that limited seasonal assessments may lead to misinterpretation of forest roads by mammals. We emphasize the need for further research to characterize the motives behind mammalian use of forest roads accurately.

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Author Contributions

M. Suzuki and M.U. Saito designed the study, M. Suzuki conducted data collection and analyses, and M. Suzuki and M.U. Saito wrote the manuscript. Both authors have accepted responsibility for the entire content of this submitted manuscript and have approved its submission.

Literature

Baltrūnaitė L. 2006: Diet and winter habitat use of the red fox, pine marten and raccoon dog in Dzūkija National Park, Lithuania. *Acta Zool. Litu. 16: 46–53.*

Biodiversity Center of Japan 2012: Vegetation survey (1:25,000). *Downloaded on 02 January 2024. http://gis.biodic.go.jp/webgis/*

Chen H.L. & Koprowski J.L. 2019: Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis. *Hystrix 30: 1–7.*

Demarais S., Verschuyl J.P., Roloff G.J. et al. 2017: Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the U. S. *For. Ecol. Manag. 385: 308–330.*

Di Bitetti M.S., Paviolo A. & De Angelo C. 2014: Camera trap photographic rates on roads *vs.* off roads: location does matter. *Mastozool. Neotr. 21: 37–46.*

Dormann C.F., McPherson J.M., Araújo M.B. et al. 2007: Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography 30: 609–628.*

Droghini A. & Boutin S. 2018: Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. *Can. J. Zool. 96: 39–47.*

Drygala F., Werner U. & Zoller H. 2014: Diet composition of the invasive raccoon dog (*Nyctereutes procyonoides*) and the native red fox (*Vulpes vulpes*) in north-east Germany. *Hystrix 24: 190–194.*

Enomoto T., Saito M.U., Yoshikawa M. & Kaneko Y. 2018: Winter diet of the raccoon dog (*Nyctereutes procyonoides*) in urban parks, central Tokyo. *Mamm. Study 43: 275–280.*

Enomoto T., Watabe R. & Saito M.U. 2023: Seasonal variation in dietary patterns and trophic niche overlap among three sympatric medium-sized carnivores in a cool-temperate zone. *J. Vertebr. Biol. 72: 23021.*

Eriksen A., Wabakken P., Zimmermann B. et al. 2009: Encounter frequencies between GPS-collared wolves (*Canis lupus)* and moose (*Alces alces*) in a Scandinavian wolf territory. *Ecol. Res. 24: 547–557.*

Gese E.M., Dowd J.L.B. & Aubry L.M. 2013: The influence of snowmobile trails on coyote movements during winter in high-elevation landscapes. *PLOS ONE 8: e82862.*

Groot Bruinderink G.W.T.A. & Hazebroek E. 1996: Ungulate traffic collisions in Europe. *Conserv. Biol. 10: 1059–1067.*

Hill J.E., DeVault T.L. & Belant J.L. 2021: A review of ecological factors promoting road use by mammals. *Mamm. Rev. 51: 214–227.*

Huey L.M. 1941: Mammalian invasion via the highway. *J. Mammal. 40: 591–594.*

Iannarilli F., Erb J., Arnold T.W. & Fieberg J.R. 2021: Evaluating species-specific responses to camera-trap survey designs. *Wildl. Biol. 2021: wlb.00726.*

Japan Meteorological Agency 2020: Normal value in Tsuruoka. *Downloaded on 02 January 2024. https://www.data.jma.go.jp/obd/stats/etrn/view/nml_amd_ym.php?prec_no=35&block_no=0263&year=&month=&day=&view=*

Keken Z., Sedoník J., Kušta T. et al. 2019: Roadside vegetation influences clustering of ungulate vehicle collisions. *Transp. Res. D 73: 381–390.*

Kumagai N. & Saito M.U. 2022: Seasonal diet changes in raccoon dogs, in a cool-temperate forest in the Shonai region, Yamagata Prefecture, Japan. *Tohoku J. For. Sci. 27: 1–10. (in Japanese with English summary)*

Lacerte R., Leblond M. & St-Laurent M.H. 2022: End of the road: short-term responses of a large mammal community to forest road decommissioning. *J. Nat. Conserv. 69: 126256.*

Lambert T.D., Sumpter K.L., Dittel J.W. et al. 2014: Roads as barriers to seed dispersal by small mammals in a neotropical forest. *Trop. Ecol. 55: 263–269.*

Maxwell S.L., Fuller R.A., Brooks T.M. & Watson J.E.M. 2016: Biodiversity: the ravages of guns, nets and bulldozers. *Nature 536: 143–145.*

Ministry of Agriculture, Forestry and Fisheries 2023: Promotion of road network improvement. *Downloaded on 02 January 2024. https://www.rinya.maff.go.jp/j/seibi/sagyoudo/romousuisin.html*

Nakane A., Enomoto T. & Saito M.U. 2022: Utilization of cultivated fruits by Japanese martens and red foxes in a snowy environment: a comparison of feeding habits between rural and forest landscapes. *J. Vertebr. Biol. 71: 22028.*

Ng J.W., Nielsen C. & St. Clair C.C. 2008: Landscape and traffic factors influencing deer–vehicle collisions in an urban environment. *Hum.-Wildl. Confl. 2: 34–47.*

O'Brien T.G., Kinnaird M.F. & Wibisono H.T. 2003: Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv. 6: 131–139.*

Okawara Y. 2018: Japanese marten. In: Masuda R. (ed.), Carnivores in Japan: mammals at the top of the ecosystem. *University of Tokyo Press, Tokyo, Japan: 154–174. (in Japanese)*

R Core Team 2022: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/*

Roever C.L., Boyce M.S. & Stenhouse G.B. 2008: Grizzly bears and forestry II: Grizzly bear habitat selection and conflicts with road placement. *For. Ecol. Manag. 256: 1262–1269.*

Saito M. & Koike F. 2013. Distribution of wild mammal assemblages along an urban-rural-forest landscape gradient in warm-temperate East Asia. *PLOS ONE 8: e65464.*

Saito M., Momose H. & Mihira T. 2011: Both environmental factors and countermeasures affect wild boar damage to rice paddies in Boso Peninsula, Japan. *Crop Prot. 30: 1048–1054.*

Saito M., Momose H., Mihira T. & Uematsu S. 2012: Predicting the risk of wild boar damage to rice paddies using presence-only data in Chiba prefecture, Japan. *Int. J. Pest Manag. 58: 65–71.*

Saklaurs M. & Baltmanis R. 2014: The effect of roads on the movement of large and mid-sized mammals. *Environ. Clim. Technol. 14: 23–29.*

Sasaki H. & Kawabara M. 1994: Food habits of the raccoon dog *Nyctereutes procyonoides viverrinus* in a mountainous area of Japan. *J. Mamm. Soc. Japan 19: 1–8.*

Scalbert M., Stiernon Q., Franceschini S. et al. 2023: Not all roads are barriers: large mammals use logging roads in a timber concession of south-eastern Cameroon. *For. Ecol. Manag. 541: 120910.*

Seki Y. & Koganezawa M. 2011: Factors influencing winter home ranges and activity patterns of raccoon dogs *Nyctereutes procyonoides* in a high-altitude area of Japan. *Acta Theriol. 56: 171–177.*

St-Pierre F., Drapeau P. & St-Laurent M.H. 2022: Stairway to heaven or highway to hell? How characteristics of forest roads shape their use by large mammals in the boreal forest. *For. Ecol. Manag. 510: 120108.*

Sutor A., Kauhala K. & Ansorge H. 2010: Diet of the raccoon dog *Nyctereutes procyonoides* – a canid with an opportunistic foraging strategy. *Acta Theriol. 55: 165–176.*

Suzuki M. & Saito M.U. 2023: Forest road use by mammals revealed by camera traps: a case study in northeastern Japan. *Landsc. Ecol. Eng. 19: 289–296.*

Suzuki M., Watabe R. & Saito M.U. 2023: Forest road use by medium-sized mammals in winter snow environments in a hilly area. *Landsc. Ecol. Eng. 19: 549–557.*

Terada C., Tatsuzawa S., Kawamura T. & Fujioka M. 2010: Evaluation of forestry roads as feeding sites of sika deer. *Jpn. J. Conserv. Ecol. 15: 193–201. (in Japanese with English summary)*

van Doormaal N., Ohashi H., Koike S. & Kaji K. 2015: Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan. *Eur. J. Wildl. Res. 61: 517–527.*

Zimmermann B., Nelson L., Wabakken P. et al. 2014: Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav. Ecol. 25: 1353–1364.*

Supplementary online material

Table S1. Parameter estimates of generalized linear models (GLMMs) for Japanese martens, red foxes, raccoon dogs, Japanese hares, and wild boar.

Fig. S1. Slope angle at forest road, decommissioned road, and forest interior sites in this study area. We measured the slope angle at five-meter intervals on a 30 m line established at each site using a VertexIV (Haglöf, Sweden). To account for the effects of shaking when measuring the slope angle, we calculated the average of three measurements taken at each survey point. From this average value, taken at five-meter intervals, we calculated an average value for the entire line. For forest road and decommissioned road sites, a line was created along the road, and for forest interior sites, two perpendicular lines were created.

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