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Movements and habitat selection of a marsupial carnivore in a modified landscape

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Abstract

Landscape modification is a major threat to carnivores worldwide, but modified landscapes can also provide important habitat for these species, as protected areas alone are insufficient. Understanding how carnivores move through modified landscapes, such as production forests, can inform management strategies to improve the value of these landscapes to carnivores. Little is known about habitat selection by marsupial carnivores in production forests, where they occupy a similar ecological niche to their more well-studied eutherian counterparts. We used GPS tracking, Hidden Markov Models, and Manly's selection ratios to identify the habitat selected in 3 movement states indicating resting/feeding, foraging, and travel by the largest marsupial carnivore, the Tasmanian devil (*Sarcophilus harrisii*), in a timber plantation-dominated landscape. Devils did not show preferences for any of native forest, native grassland, and plantation in any movement state. Within plantations, devils preferred a plantation age of 4–7 years (selection ratio [*wi*] = 1.52) and slightly avoided older plantations (8–13 years *wi* = 0.74, 14+ years *wi* = 0.65). Devils preferred roads (state 1: *wi* = 2.71, state 2: *wi* = 2.48, state 3: *wi* = 2.97) and plantation edges (state 1: *wi* = 2.38, state 2: *wi* = 2.24, state 3: *wi* = 2.78) in all movement states, and moved faster on roads (0.06 [95% CI 0.04 to 0.09] $m.sec^{-1}$) and edges (0.08 [0.06 to 0.10] $m.sec^{-1}$) than away from them, indicating they use them for foraging and travel. No measured habitat variables influenced devil home range size. To support devils in plantation landscapes, we recommend maintaining a heterogeneous landscape of different plantation ages and native remnants and reducing the risk of vehicle collisions by minimizing forestry traffic at night. Tasmanian devils share similar adaptable traits to generalist eutherian carnivore species in their use of modified landscapes. Plantations can provide valuable habitat for this and other threatened predator species.

Keywords

plantation, Tasmanian devil, forestry, GPS telemetry, roads, edges, foraging, production forest

Background

With the ongoing global loss of untouched forests (1), there is increasing focus on finding strategies to preserve and also enhance biodiversity in human-modified landscapes (2). Modified habitats such as production forests can make an important contribution to maintaining forest ecosystems, as protected areas alone are insufficient (3). For instance, replacing native forests with timber plantations (henceforth 'plantations') negatively affects forest biodiversity (4), but plantations often contain higher biodiversity than other land uses such as agriculture, and can decrease harvesting pressure on native forest (2). Conservation strategies in production forests should be informed by ecological research to maximize effectiveness and cost-efficiency (5).

Carnivores are especially sensitive to modified landscapes (6) and knowledge of their habitat use within these landscapes can inform practices to sustain their populations. This is particularly important as carnivores have key ecological effects such as limiting populations of prey and smaller predators (7), effects that are dampened in modified landscapes (8). Improving carnivore conservation in anthropogenic landscapes such as production forests can therefore benefit entire ecosystems in these landscapes. Carnivore species can differ markedly in both their habitat selection within plantations (9,10) and their responses to forestry operations (11). While the use of production forests by eutherian carnivores has been well studied (12), little is known about the use of these landscapes by marsupial carnivores, which occupy a similar ecological niche and face comparable threats from habitat loss (13).

As well as displaying broad preferences among habitats, carnivores may also show finer scale differences in the habitats used for different behaviors, such as travel, foraging and denning

(14). Understanding carnivore movements within these landscapes can help elucidate these behaviors and highlight important habitat characteristics (15). Animals often change their movements in response to altered forest structure (16). Habitat features such as windrows (linear piles of logging debris) (17) and corridors (18) can facilitate animal movement across production forest landscapes, and plantations can connect patches of native forest (19). Anthropogenic linear features in production forest landscapes, such as roads and edges between natural and modified vegetation, can be used by carnivores for travel and hunting (20,21) but also expose them to threats such as vehicle collisions (22). Investigating how carnivores move through production forestry landscapes, and the behaviors influencing habitat selection, can inform management strategies to promote important habitat features in the landscape.

With plantation forest cover in Australia increasing, fauna conservation is an important consideration in plantation management (23). This is particularly relevant in Tasmania where plantations comprise nearly 10% of total forest cover (24), and thus have significant potential to supplement native forest habitats and contribute to maintaining ecological function of the broader Tasmanian forest ecosystems if managed with conservation in mind.

Tasmania is home to the world's largest marsupial carnivore, the Tasmanian devil. Devils are endangered due to a rare transmissible cancer, devil facial tumor disease (DFTD) (25), that has caused a steep population decline of over 80% since 1996 (26), leaving them vulnerable to other threats. Devils play multiple important roles in Tasmanian ecosystems: as morphologically specialized scavengers, they influence carrion persistence in the landscape (27), and as top predators, they help maintain trophic function and suppress feral cats (*Felis catus*) (28). Finding ways to protect devils in human-modified landscapes is a priority to maintain ecosystem function. Previous research investigated devil use of anthropogenic pastoral landscapes, finding that devils foraged along the pasture-forest interface and used

pastures mainly for travel (29). Another study found devil abundance increases with plantation extent in production forest landscapes (30). Movements and habitat selection by devils in plantations have not been studied.

Our study provides the first analysis of marsupial carnivore habitat selection and movements within plantations, complementing similar research on eutherian carnivores, and enhancing our understanding of carnivore use of production forests. We used GPS tracking to explore the use of a plantation landscape by devils, with the intent to provide recommendations for plantation managers to sustain devil populations. We focused mainly on adult female devils, a key demographic to protect in critically diminished populations, particularly when they are raising young (April to January) (31,32). We aimed to answer 3 questions:

1. At a plantation landscape scale, how do female devils select among habitat types for different behaviors, and how do different habitats influence devil home range sizes?
2. At a plantation-specific scale, how do female devils select among plantation ages for different behaviors?
3. How do devils move through plantation landscapes?

Methods

Study area

This study was undertaken in Surrey Hills, a eucalypt plantation landscape in northwest Tasmania (-41°S, 145°E) (Figure 1). The site is embedded in an intensively managed forestry region containing a mosaic of *Eucalyptus nitens* plantation stands of varying ages and remnant native forest and grassland patches. It has an average annual rainfall of 2,163 mm and mean maximum temperature of 12.3°C (33). The plantations have mostly been established since the mid-1970s on previously native vegetation land, and the remaining

native vegetation primarily comprises highland *Poa* spp. grasslands, *Eucalyptus delegatensis* grassy forests and cool-temperate rainforest dominated by *Nothofagus cunninghamii* (34). DFTD has been present in the landscape for about 6 years, causing steep population declines of devils (26).

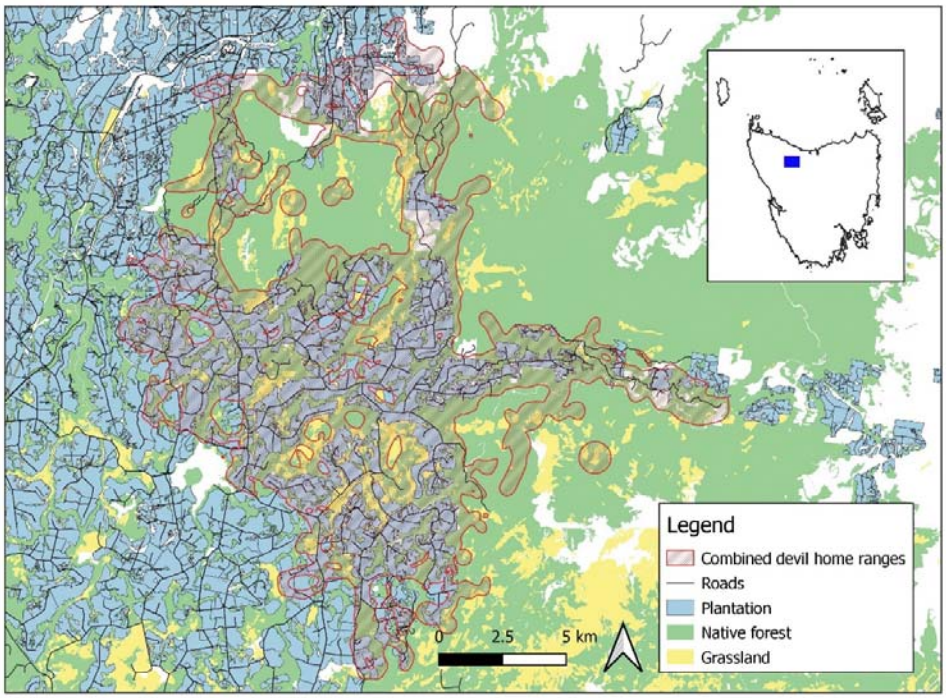

Figure 1: Study site within Tasmania (inset), overlaid with the combined home ranges of all devils in the study (95% utilization distribution from Biased Random Bridges).

GPS telemetry

We captured adult devils (> 2 years old) in custom-built traps (made from 80 cm by 30 cm PVC pipe) and fitted them with GPS radio-collars (Q4000ER GPS, Telemetry Solutions, Concord USA) between April-October 2021. Collars weighed 140 g, less than 3% of the body weight of collared individuals, and were fitted with corrosive bolts that degrade over time and eventually allow the collar to drop off (35). As devils are primarily nocturnal (36), collars were set to take 15 minute fixes every second night from approximately sunset until

sunrise (17:30 to 07:00 April and August, 17:00 to 07:30 May to July, 18:00 to 06:00 September, 18:30 to 05:30 October) and were turned off during the day to conserve batteries. We set 'GPS additional time' to 30 seconds, which forces the GPS unit to keep searching for satellites even after it acquires a fix, improving fix accuracy. Collars were also equipped with a VHF unit to assist with relocation.

GPS data screening

To account for errors in animal locations acquired by the GPS, fixes with less than 3 satellites, horizontal dilution of precision (HDOP) > 7 (as in Andersen et al. [29]), or unrealistic step lengths (> 4000 m) were removed from the analysis. Lower values of HDOP indicate higher location precision. Because the successful fix rate was low, we tested for bias in the success rate of GPS fixes due to vegetation type or plantation age. First, we left 10 collars stationary overnight in each of 3 vegetation types – native forest remnant, 1–5 year old plantation, and 10–15 year old plantation – and compared percentages of successful fixes among habitats. Second, we used straight-line interpolation to approximate the locations of failed fixes ('approx' function in R package 'stats') and compared the percentages of points in native forest, plantation and native grassland between real and interpolated points. Interpolated points were not used for analysis.

To see how many failed GPS fixes could be attributed to animals resting in a den, ambient temperatures recorded by the collars were plotted and compared between successful and failed fixes. Temperatures > 25°C appeared to indicate animals were in a den. Collar temperatures were unlikely to reach 25°C while animals were active since fixes were programmed only at night, and devils were collared over winter and spring in a relatively cold climate (annual mean max temp 12.3°C [33]).

Home ranges

We calculated devil home ranges using biased random bridges (BRBs) (37), which quantify an animal's utilization distribution (UD) based on movement paths rather than just the density of individual fixes. We identified 95% UDs for each individual devil. Home ranges were also estimated using 100% minimum convex polygons (MCPs) (38) for comparison with the broader literature. This is a commonly reported method of home range estimation, though it is prone to overestimating the areas actually used by animals (39,40). We did not use kernel density estimates (KDEs) (41), another widely used method, as the limited data and decentralized spread of GPS points for many individuals made this method unsuitable for our study. Analyses were carried out using the 'adehabitatHR' package in the R programming environment (42).

We constructed maps of the study site using vegetation data from the TasVeg 3.0 layer (43) and plantation features provided by the landowners, Forico Pty Ltd. Vegetation classes were grouped into 3 habitat types: plantation, native forest, and native grassland (including moorland and scrub). Plantation ages were grouped into 5 classes: < 1, 1–3, 4–7, 8–13 and 14+ years, age classes used by the forest industry due to different fuel loads. To examine if habitat variables influenced devil home range size (95% UDs), linear models were constructed using home range size as a response variable and proportions of different habitat types and plantation ages within each devil's UD as predictors. These variables were included in separate models as proportions of different habitats/plantation ages would be correlated with one another, and plantation ages would be correlated with the percentage of plantation. Sex was also used as a predictor variable, both alone and in combination with other variables. We selected final candidate models using Akaike's Information Criterion values adjusted for small sample size (AICc) (44) according to the methods of Richards (45), where models with ΔAICc > 6 were excluded, as were more complex models where simpler, nested models had smaller AICc values. To identify how much of the devils' home ranges were affected by

recent and active logging, and infer how this may influence their behavior, we calculated the percentage of each devil's home range that was logged during the collaring period (April to October 2021) and in the 12 months preceding it.

Movement states

To identify different movement states of female devils that may influence their habitat selection, we classified the GPS fixes for each animal into 3 different movement states using Hidden Markov Models (HMMs) (46). This method classifies movement paths according to differences in turning angle and step length between successive locations, and assumes that these characteristics are driven by underlying behaviors. Movement states can therefore approximate behavioral states to some extent. We used past HMM results from devils to guide our choice of initial parameters for each state (47) (see Supplementary Table 1, Additional File 1): state 1, stationary (e.g., resting and/or feeding at carcass); state 2, characterized by short step lengths and variable turning angles indicating tortuous movement (e.g., foraging); and state 3, characterized by long step lengths and relatively constant turning angles indicating directional movement (e.g., travel). Analyses were carried out using the 'moveHMM' package in R (48).

Sequential GPS tracking data are often temporally autocorrelated which can violate assumptions for statistical inference (49). To account for this, once movement states were assigned to all GPS fixes, we used variograms (function 'variogram' in R package 'ctmm' [50]) for individual devils in each state to find a time threshold at which variance stabilized and each location could be considered independent. We subsampled the GPS data by the time threshold specific to each movement state (function 'track_resample' in R package 'amt'; [51]) and used the subsampled data for habitat selection analysis. We did not have sufficient data to analyze selection of plantation ages by different movement states, so for plantation-

specific habitat selection analyses, we repeated this process and subsampled the data by the time threshold for all combined states.

Habitat selection and animal movements

For landscape-scale habitat selection analyses and for the plantation-specific analyses, we used the same 'habitat type' categories and 'plantation age' classes, respectively, as above. To investigate how animals may use plantation edges (edges between plantation and other habitat types, excluding roads) and roads for movement and foraging, we created 3 buffer zones around plantation edges and roads: < 20 m (on roads/edges, as in Andersen et al. [29]), 20–50 m (near roads/edges) and > 50 m (away from roads/edges). We calculated the percentage of each habitat type, plantation age class, and road/edge buffer in each devil's 95% MCP (to reduce undue influence of outlying points), buffered by 5%, to represent available habitat. We used MCPs to define available habitat as we needed to measure all potentially available habitat rather than just the areas used by the animal. For each successful GPS point within the buffered MCPs we identified the habitat type, plantation age class (if applicable), and their distance to plantation edges and roads, split into the above buffers. These calculations were performed in QGIS 3.14®.

We used Manly's selection ratios to investigate habitat selection by female devils in each HMM movement state, a method that tests for differences in used vs. available habitat (52). As there were insufficient male devils to examine sex differences in habitat selection, the 3 male devils were excluded from this analysis. We used a design III analysis, which recognizes that the available habitat differs among individuals (52). The selection ratio is the proportional use divided by proportional availability of each habitat attribute class, with a selection ratio (*wi*) > 1 indicating that a habitat type was used proportionally more than expected based on availability and < 1 proportionally less. The percentages of habitat

attributes within buffered MCPs represented available habitat, while the locations of GPS points within the buffered MCPs represented used habitat. Univariate models were run for each movement state with the predictors of habitat type, plantation age, and distance to roads and plantation edges. Analyses were undertaken using the 'adehabitatHS' package in R (53).

Velocity

To support movement state analyses and help clarify devil movements in different habitats, we calculated the velocity of each devil at each GPS point using the difference in time and distance between 2 consecutive points using the 'sp' package in R (54). GPS points following a failed fix were ignored. The distance from each GPS point to the nearest road and plantation edge was calculated in QGIS 3.14® and classified into 'on road/edge' (< 20 m), 'near road/edge' (20–50 m) and 'away from road/edge' (> 50 m). We tested for correlation between the values for plantation edges and roads using a polychoric correlation test (function 'polychor' in package 'polycor' in R) and found low correlation (0.36), so these variables could be included in the same model. To investigate if devils move at different speeds in different habitats, we constructed linear mixed effects models using 'velocity' as a response variable and distance to road, distance to edge, habitat type, and plantation age as predictors. Animal ID was included as a random effect. We ran 2 sets of models: 'whole-of-landscape' models, including all successful GPS fixes and all predictors except plantation age; and 'plantation-only' models, including only GPS fixes inside plantations, and all predictors except habitat type (to investigate the influence of plantation age). Final candidate models were selected using the same process as for the home range models (44), using AIC for whole-of-landscape models and AICc for plantation-only models.

Results

We deployed GPS radio-collars on 15 adult devils (12 females, 3 males) between April and October 2021. One collar was unable to be retrieved at the end of the study, though some data were downloaded when the animal was recaptured during the study. A total of 7406 successful GPS fixes remained after removal of GPS errors, a success rate of 23% (successful vs programmed fixes). After accounting for temperatures recorded by the collar that indicated the animal was in a den (> 25 °C), the fix success rate increased to 52%, indicating much of the missing data was due to devils being in underground burrows where the collars could not detect satellites. Data were retrieved from between 24 and 164 days per animal (mean 77 ± 49 SD), with 152 to 1452 successful fixes per individual (494 ± 384) (see Supplementary Table 2, Additional File 1). A total of 7066 points were used for analysis, following removal of points outside each animal's buffered 95% MCP.

The stationary collar test had a fix success rate of 99% in plantation age 1–5 years, 97.2% in age 10–15 years, and 93.6% in native forest, similar to the difference in fix success rate among habitats in other studies (29). Comparison of the proportion of real vs. interpolated fixes that fell in each habitat category showed little difference between habitats (native forest 45.7% and 45.8% respectively, plantation 43.8% and 45.5%, grassland 10.4% and 8.8 %), indicating that any difference in fix success rate among habitats did not introduce a significant bias, though there was considerable variation among individuals (see Supplementary Table 3, Additional File 1).

The best performing HMM differentiated the 3 movement states as: state 1, representing little or no movement, with a mean step length of 16.37 ± 13.09 m (± SD) and a wide distribution of turning angles centered on 3.13 rad (concentration 0.39); state 2, with intermediate step lengths of mean 177.84 ± 148.25 m and a wide distribution of turning angles centered on 0.03 rad (concentration 0.52); and state 3, with longer steps of mean 527.03 ± 228.58 and a narrow distribution of turning angles centered on 0.03 rad (concentration 1.66), suggesting faster

directional movement (see Supplementary Figure 1, Additional File 1). GPS data variance stabilized and temporal autocorrelation decreased around 3 hours for state 1 and combined states, and 4 hours for states 2 and 3. Data were subsampled by these state-specific time thresholds for habitat selection analysis, leaving 338 observations for state 1, 469 for state 2, 712 for state 3, and 859 for combined states. All HMM results can be found in Supplementary Table 4, Additional File 1.

Landscape-scale habitat selection and home ranges

At a landscape scale, behavior-specific habitat selection ratios for female devils showed that devils did not select among habitat types (plantation, native forest, and native grassland/scrub) in any movement state (state 1: $p = 0.48$, state 2: $p = 0.69$, state 3: $p = 0.56$) (Figure 2a).

Home range sizes (95% UDs from BRBs) were a mean of 1849 (416 SE) ha for female devils and 3343 (1388 SE) ha for males. Core use areas (50% UDs) were 318 (66 SE) ha for females and 467 (102 SE) ha for males. 100% MCPs were a mean of 3481 (1475 SE) ha for females and 6326 (4401 SE) ha for males. UD and MCP estimations for individual devils can be found in Supplementary Table 2, Additional File 1. A single model remained in the final candidate set for predictors of devil home range size (95% UDs) and included only sex (**Error! Reference source not found.**). Home ranges of males were 1494 (95% CI 566 to 2421) ha larger than females. The average recently logged area within each devil's home range was 3.46% (0–9.15%, see Supplementary Table 1, Additional File 1). Male home range results should be treated with caution as there were only 3 male devils in the study.

Home range size (ha)

Fixed effects		Model description	
Intercept	Sex	df	AICc
1849 [1433 to 2264] (female)	1494 [566 to 2421] (male)	3	234.6

Velocity (m.sec^{-1}) (whole-of-landscape)

Fixed effects			Random effects		Model description	
Intercept (m)	Distance to road (m)	Distance to plantation edge (m)	Intercept (animal ID)	Residual	df	AIC
0.41 [0.38 to 0.44] (< 20)	-0.09 [-0.12 to -0.06] (20–50) -0.06 [-0.09 to -0.04] (> 50)	-0.07 [-0.09 to 0.05] (20–50) -0.08 [-0.10 to -0.06] (> 50)	0.002 (0.04 SD)	0.09 (0.30 SD)	5	2511.3

Table 1: Final candidate models with parameter estimates for predicting devil home range size and velocity in plantations (95% CIs in square brackets []).

Plantation-specific habitat selection

Within plantations, habitat selection ratios for female devils indicated devils used plantations of different ages non-randomly ($p < 0.001$). Female devils selected for age 4–7 years (*wi* = 1.52 [95% CI 0.98–2.05]), slightly avoiding older age classes 8–13 (*wi* = 0.74 [0.28–1.20]) and 14+ years (*wi* = 0.65 [0.16-1.15]) and neither selecting nor avoiding young age classes < 4 years (Figure 2b).

Devil movements in plantation landscapes

Female devils selected habitats non-randomly in all movement states regarding distance to roads (state 1: $p = 0.1$, state 2: $p = 0.01$, state 3: $p < 0.001$) and plantation edges (state 1: $p < 0.001$, state 2: $p < 0.001$, state 3: $p < 0.001$) (Figure 2c). Female devils used areas < 20 m from plantation edges (state 1: *wi* = 2.38 [95% CI 1.66–3.10], state 2: *wi* = 2.24 [1.63–2.85], state 3: *wi* = 2.78 [2.09–3.46]) and roads (state 1: *wi* = 2.71 [1.38–4.05], state 2: *wi* = 2.48 [1.59–3.37], state 3: *wi* = 2.97 [2.10–3.82]) more than twice as often as expected for all states. To a lesser extent, they selected for areas 20–50 m from plantation edges (*wi* = 1.47 [95% CI 1.11–1.82]) and roads (*wi* = 1.69 [1.19–2.20]) for state 2 only. They avoided areas > 50 m from edges (state 1: *wi* = 0.68 [95% CI 0.47–0.89], state 2: *wi* = 0.64 [0.49–0.79], state 3: *wi* = 0.62 [0.49–0.75]) and roads (state 1: *wi* = 0.87 [0.79–0.95], state 2: *wi* = 0.87 [0.81–0.92], state 3: *wi* = 0.89 [0.83–0.96]) in all states, particularly edges.

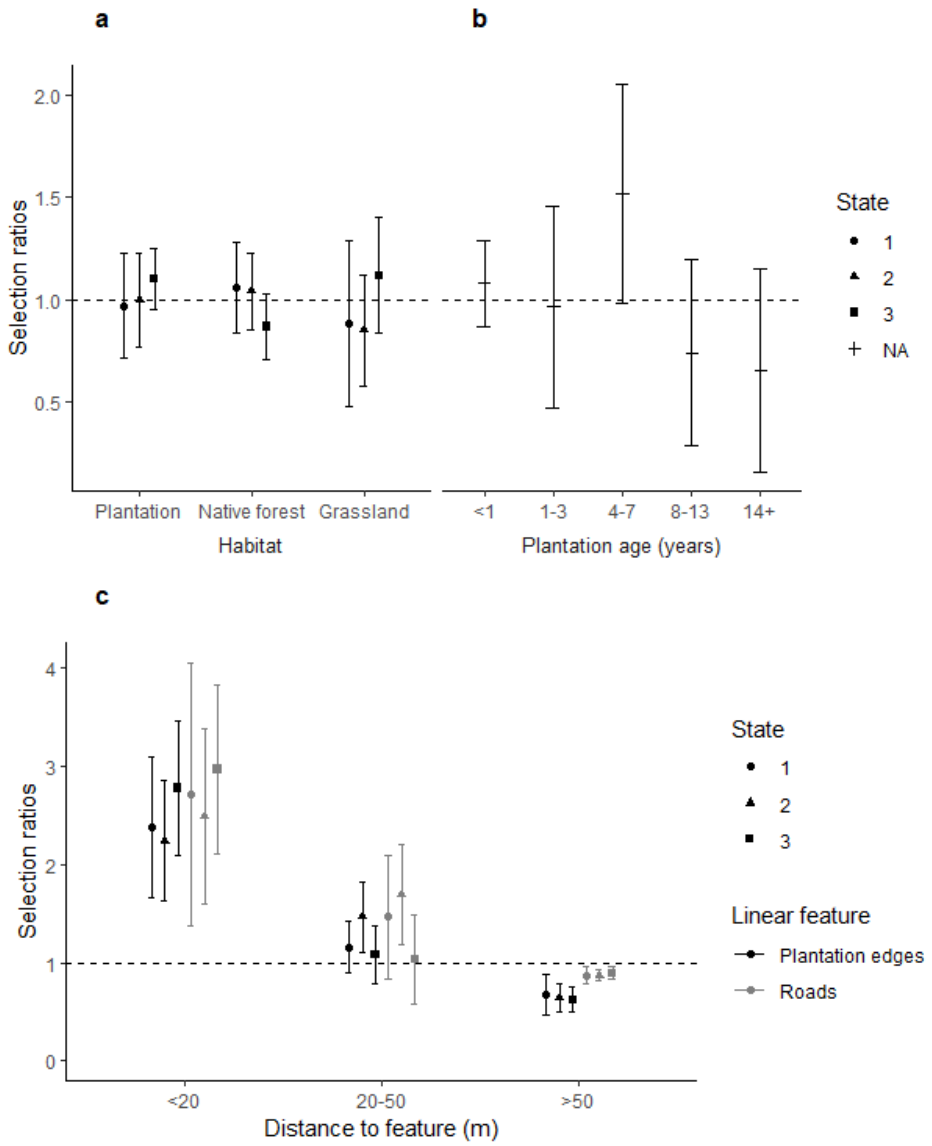

Figure 2: Habitat selection by adult female devils regarding habitat type (a), plantation age (b) and distance to roads/edges (c) in 3 movement states. Movement states were not considered for plantation ages due to limited data. Error bars show 95% CIs. A selection ratio of 1 indicates attributes were selected in proportion to availability; 0.5 indicates they were used half as often as expected; and 2 indicates they were used twice as often as expected, based on availability within buffered 95% MCPs.

A single model remained in the final whole-of-landscape candidate set predicting devil velocity and this model included both distance to roads and plantation edges (**Error! Reference source not found.**). Devils moved faster on roads and edges (< 20 m) than away from them (Figure 3). In the plantation-only models, only distance to plantation edges

remained in the final candidate list (see Supplementary Table 5, Additional File 1). As plantation-only models used a subset of the whole-of-landscape data and the results were similar, we consider whole-of-landscape results more relevant for interpretation.

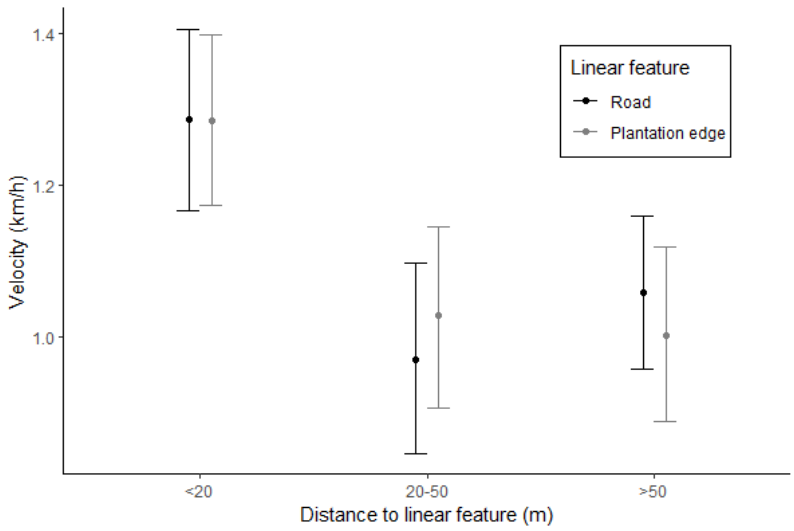

Figure 3: Predicted velocity of devils with distance to roads and plantation edges using whole-of-landscape data. Error bars represent 95% CIs.

Discussion

Our results demonstrate the adaptability of devils to human-modified landscapes, highlighting the need to manage these landscapes as valuable devil habitat. Devils did not show preferences among different habitat types at a landscape scale, though at a finer scale they showed selection for specific plantation ages, and they preferentially used plantation edges and roads to hunt and to move through the landscape.

Landscape-scale habitat selection and home ranges

At a landscape scale, female devils did not show selection among plantation, native forest remnants, and native grassland in any movement state, and no habitat attributes considered affected devil home range sizes. This demonstrates the adaptability of devils to human-modified landscapes, consistent with Jones et al. (30)'s finding that devil abundance slightly

increased with plantation extent in production forest landscapes. Devils are generalist carnivores (29), and generalist species usually respond more positively to human-modified landscapes than specialists (55). Other generalist carnivores such as raccoon dogs (56) even use plantations to a greater extent than native forest. Plantations likely provide abundant prey for devils. Medium-sized herbivores, wallabies and pademelons (Family Macropodidae; *Macropus rufogriseus* and *Thylogale billardierii*), and brushtail possums (*Trichosurus vulpecula*), preferred devil prey (57), are common enough in Tasmanian plantations that they are regularly culled to protect seedlings (24). Culling along with roadkill from forestry vehicles would provide abundant carrion for this specialized scavenger (58). There appear to be sufficient resources available in these landscapes for an opportunistic predator and facultative scavenger to exploit.

Notably, home ranges of devils in this study were substantially larger than those in Andersen et al. (59) (100% MCPs: females 2072 [277 SD] ha, males 3105 [309 SD]), which was conducted in an area that was free of DFTD at the time of the study and contains a mix of conservation and agricultural land. This is surprising as female devils decreased their home range sizes in another landscape that suffered significant population decline due to DFTD (60), likely due to less competition for resources. In the present study, we would therefore expect smaller home range sizes than in Andersen et al. (59) due to low devil density in our study landscape caused by high DFTD mortality (26). As home range size tends to increase with lower quality habitat (61), this result may indicate that the plantation-dominated landscape in our study area was less ideal devil habitat than the more protected landscape in Andersen et al. (59). Perhaps protected landscapes provide more spatially and temporally constant and reliable resources (e.g., prey and den sites) than a production forest landscape that is always changing due to harvesting. For instance, black bears (*Ursus americanus*) were

found to have larger home ranges in plantation dominated than in unmanaged forest landscapes (62).

Plantation-specific habitat selection

Within plantations, female devils selected for plantation aged 4–7 years and avoided older plantations. Younger plantations may contain a higher density of wallabies and brushtail possums which browse in plantations (63). Some other carnivores, such as American marten (*Martes americana*) (64), similarly prefer younger post-logging native forest, likely due to prey availability. Additionally, near-surface vegetation cover in hardwood plantation, e.g., grass and shrubs, increase with plantation age in Tasmania (K. Parkins, pers. comm.), which may create a dense understory layer that restricts movement for devils in older plantations. While many carnivores prefer dense understory in plantations (11,65), this is often to avoid other predators or stalk prey. Devils are pounce-pursuit predators, capable of fast but short pursuit but dependent on some degree of ambush to get sufficiently close (58). They prefer forested rather than open environments and use forest edges to intercept herbivore prey as they move between daytime refuges and open areas to feed at night (29,66). The habitat structure offered by young plantations 4–7 years old may provide sufficient cover to conceal them from prey but not enough to significantly obstruct movement and potentially impede hunting and prey capture. Very young plantations may be too open for devils to be able to effectively ambush prey which could see them coming and move out of range.

It is interesting that female devils did not appear to avoid recently logged plantation (< 1 year), although this result was based on just 4 individuals. Considering female devils likewise did not avoid plantations 1–3 years old and actively selected for 4–7 years old, and that plantation forestry landscapes have high prey abundance, logging is unlikely to have a long-term negative effect on devil use of the landscape, as long as it is on a schedule that maintains

plantation age heterogeneity in the landscape. Furthermore, as we found female devils avoided older plantation, logging removes habitat that is already apparently nonpreferred (coupes are logged at ~12–15 years old in this landscape). Other factors likely to influence the effect of logging on devils include the quality of remaining habitat in the surrounding area and home range (e.g., plantation ages and native forest remnants) (23); the timing of logging i.e., if logging occurs during the maternal denning season and could disrupt denning behavior; and the overall area and proportion of home range harvested (67). We could not directly investigate how devils responded to active logging, however, the proportion of their individual home ranges that was logged during the study and in the preceding year was small (mean 3.5%, range 0–9%), so even short-term displacement due to logging may not have had a major effect on devils in this study. Extrapolation of these results to other years and landscapes should be treated with caution due to variations in logging area size and intensity. The lack of an apparent response to logging by devils is particularly surprising as the logging method in the landscape is clearfelling, which involves removing all trees from the harvest footprint and typically has a more negative effect on biodiversity than other logging methods (68). Some carnivores can respond positively to clearfelling in plantations, however, perhaps due to increased prey availability (69).

Devil movements in plantation landscapes

Devils preferentially used roads and plantation edges to move through the landscape in all movement states. This is consistent with Andersen et al. (29)'s discovery that devils use anthropogenic linear features for movement and foraging. Devils moved faster on roads and edges, indicating they use them for travel. Edges of plantation coupes are cleared of trees to allow vehicle access, potentially providing less obstructed movement paths for devils. Other carnivores such as wolves similarly use linear features such as roads and seismic lines for travel, allowing them to move further and faster (70). Our results indicate devils also forage

along roads and edges. As well as scavenging roadkill along roads (29), devils may use plantation edges to intercept macropod prey moving between the denser shelter of native forest where they rest during the day to browse in more open plantations at night (63), as was found for the forest-pasture interface in Andersen et al. (29). Other carnivores likewise select for edges in production forest landscapes (14,71), which can increase hunting success (20). Female devils selected for areas close to (20–50 m), but not on, roads and edges for state 2 only. State 2 represents shorter, more tortuous movements which may indicate foraging, contrasted with longer, straighter step lengths for state 3 which suggests travel, and stationary behavior in state 1, i.e. resting or feeding at a carcass. Selection of areas 20–50 m from roads/edges in state 2 may be explained by devils searching for food near roads/edges but in cover to intercept prey, combined with a higher chance of picking up scents of prey or carcasses that are close to roads/edges while travelling along them.

Management implications

As plantations appear to be valuable habitat for devils, we recommend implementing strategies to maintain habitat suitability for devils in plantation landscapes. Preserving a heterogeneous landscape with a mosaic of different plantation ages – along with patches of native vegetation remnants (23) – is likely to benefit devils due to their broad use of different habitat types and their preferences among plantation ages. The use of plantation landscapes by devils exposes them to potential risks from human use of the landscape such as timber harvesting operations, vehicle collisions, and lead poisoning from consuming culled browser carcasses (72). Our finding that devils preferentially use roads make them particularly vulnerable to vehicle collisions, a major cause of devil mortality (22). Logging in some coupes occurs during 24 hours in this landscape. Since measures targeted at changing driver behavior such as implementing speed limits and increasing driver awareness have limited effectiveness (22), the most effective way to mitigate this risk to devils may be to minimize

forestry traffic at night. Our study suggests that the risk to devils from harvesting operations is likely to be minimal, as devils slightly avoided the plantation age class most likely to be harvested (14+ years), and the age class they preferred (4–7 years) is unlikely to be harvested. One caveat is that we were unable to investigate denning behavior of devils in this study, so the risk of damage to devil dens during logging operations – particularly maternal dens, which may harbor young devils unable to escape – remains unknown.

Conclusions

Our study reinforces the high adaptability of devils to human-modified landscapes (29), similar to other generalist carnivores (12). Not only did devils show no selection between plantation and native habitat remnants, they took active advantage of modified habitat features – edges and roads – for foraging opportunities and expediated travel. Similar behavior has been observed before in devils (29) as well as other carnivores (70). Habitat selection by carnivores in production forests is highly variable among species, such as selection among harvested forest ages: some carnivores, like devils, prefer young-mid stage regrowth (73), while others select for mature forest (74). Identifying species-specific habitat selection in human-modified landscapes is therefore important. While it is essential to recognize that carnivores as a group are particularly vulnerable to human impacts (6), it is also important to understand that many generalist carnivores are adaptable to modified landscapes, providing impetus to manage these landscapes as valuable habitat for these species. Production forests are an excellent example – they are often incorrectly viewed as of little value to conservation, exposing them to mismanagement and habitat degradation (2). Recognizing that production forests and other modified landscapes provide important habitat to devils and other carnivores is key to maintaining populations of these predators beyond protected areas.

List of abbreviations

Devil facial tumor disease (DFTD)

Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Declarations

Ethics approval

This work was carried out under a permit from the University of Tasmania's Animal Ethics Committee (permit number 23211).

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

EJ was a major contributor in designing the study, acquiring funding, conducting fieldwork for data collection, analysing the data and writing the manuscript. AK, DM, MJ and RH were major contributors to study design. RH assisted with fieldwork issues. JP and MJ were major contributors to data analysis. All authors contributed to writing the manuscript.

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