



Considering behavioral state when predicting habitat use: Behavior-specific spatial models for the endangered Tasmanian wedge-tailed eagle

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ABSTRACT

Effective planning for species conservation often requires an understanding of habitat use. The resources an animal selects within the landscape relate to its behavioral state and, therefore, incorporating behavior into habitat selection analyses can help inform management of threatened species. Here we present an approach for developing behavior-specific spatial habitat-use models using large quantities of GPS telemetry data. Using hidden Markov models, we first characterize 231,478 GPS fixes from 22 recently fledged endangered Tasmanian wedge-tailed eagles (*Aquila audax fleayi*) as reflective of either perching, short-distance flight, or long-distance flight. We then use a multivariate habitat selection ratio to develop spatial models predicting where these behavioral states occur. Recently fledged Tasmanian wedge-tailed eagles selected for areas close to forest edges during perching and short distance flights, whereas they selected more strongly for areas with steep topography (slopes > 15°) and further from forest edges for longer flights. Models using distance to forest edge and topographic slope effectively predicted where eagles engaged in long flights ($R^2 > 0.91$, $r_s > 0.90$) in each of six regions, whereas the performance varied by region for models describing perching ($R^2 = 0.43\text{--}0.97$, $r_s = 0.80\text{--}0.97$) and short flights ($R^2 = 0.34\text{--}0.93$, $r_s = 0.63\text{--}1.00$). Our study provides a detailed understanding of habitat use by young Tasmanian wedge-tailed eagles, which has multiple applications in the ongoing conservation of the population. Our method illustrates a framework for spatially explicit and behavior-specific habitat selection analyses that can be applied to other species of conservation concern.

1. Introduction

Planning effective in situ conservation management often requires an understanding of the resources that animals use. Resource selection analyses can both describe and predict how animals use different habitats, and have thus become important tools in balancing conservation with expanding human footprints (Johnson et al., 2006; Manly et al., 2002; Thurfjell et al., 2014). These methods facilitate understanding of the importance of different habitat resources, and the prediction of where animals are likely to occur within the broader landscape (Johnson et al., 2004). The spatial delineation of resource selection can then be used to assess impacts of changes in land use (Sawyer et al., 2006), guide the design and management of ecological reserves (Leroux et al., 2007),

target reintroduction sites (Klar et al., 2008), and help identify and mitigate areas of human conflict, such as disturbance (Seip et al., 2007) and anthropogenic mortality (Meisingset et al., 2014; Miller et al., 2014; Reid et al., 2015).

Habitat selection models do not traditionally take behavior into account, rendering them susceptible to biased inferences of resource use (Roever et al., 2014). The way an animal selects habitats in the landscape may vary substantially due to the distinct resource requirements of different behavioral states. For example, the resources required for foraging, resting, and reproduction are likely to be disparate and potentially opposing. Habitat selection models that lack a behavioral component may therefore fail to identify habitats that are highly important to infrequent behaviors, while opposing habitat requirements

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during different behaviors can, within a statistical model, effectively cancel each other out (Abrahms et al., 2016; Bouyer et al., 2015; Roever et al., 2014).

The ability to resolve this issue by connecting habitat selection to natural behavior has been limited by practical constraints of observing behavior over long periods of time and without observer presence affecting behavior (Mahoney and Young, 2017). However, the increasing temporal resolution of modern GPS-tracking technologies, together with advances in statistical techniques, are facilitating a more detailed understanding of animal behavior alongside habitat use. Frequent GPS relocations can identify explicit patterns in movement, from which statistical techniques can be used to infer different behavioral states, such as foraging, resting or travelling (Morales and Ellner, 2002; Patterson et al., 2009). These behavioral states can be used in conjunction with resource selection analyses to give insight into behaviors of particular significance to conservation management. For example, through behavioral space use modelling, Patterson et al. (2016) clarified how mammals and birds use marine reserves for foraging, Miller et al. (2014) were able to identify where eagle flights are likely to coincide with a high risk of wind turbine collisions, and Sur et al. (2021) linked behavioral states to habitat features in the context of development of infrastructure for solar energy extraction. Incorporating behavior into resource selection analyses can therefore be particularly useful in guiding the management of species reliant on conservation actions.

Here we present an analytical approach for spatially explicit and behavior-specific habitat selection studies using high temporal-resolution GPS tracking data from Tasmanian wedge-tailed eagles (*Aquila audax fleayi*). The Tasmanian wedge-tailed eagle is an endangered (Commonwealth of Australia, 1999) subspecies endemic to the island of Tasmania. With the loss of the thylacine (*Thylacinus cynocephalus*) and recent declines in populations of Tasmanian devils (*Sarcophilus harrisi*), the wedge-tailed eagle serves a particularly important ecological function as one of the few remaining top predators in Tasmanian ecosystems. However, the population faces a series of threats, including habitat loss, low reproductive rates linked to nest disturbance, and high rates of human-caused mortality due to exposure to environmental contaminants, persecution, and collisions with automobiles, power lines, and wind turbines (Bekessy et al., 2009; Forest Practices Authority, 2017; Garnet and Baker, 2020; Mooney and Holdsworth, 1991; Pay et al., 2021, 2020; Threatened Species Section, 2006). The number of collisions with powerlines and wind turbines is expected to increase with the growing development of wind energy in Tasmania and electrical infrastructure to service expanding residential and industrial developments (Bell and Mooney, 1998). Since risk is behavior specific (e.g., collision with an automobile is less likely during long-distance movements at high altitude than when stationary and feeding on roadkill), spatially explicit models showing where Tasmanian wedge-tailed eagles are likely to perform different behaviors can guide integrated planning and management at the landscape level to mitigate for these stressors.

Our framework involves (1) categorizing GPS-tracking data into distinct behavioral states using derived movement attributes, (2) identifying the habitat associations for each of the behavioral states, and (3) using this information to develop spatial models that predict where different behaviors are likely to occur in the landscape. Validation of the predictive capacity of maps produced by habitat selection analyses is often neglected (Johnson et al., 2006), even in conservation settings. We therefore conclude by (4) using a leave-one-out cross-validation (LOOCV) method to assess the predictive capacity of the spatial models by individual and region.

2. Methods

2.1. Study area & focal species

The study was conducted in Tasmania, an island state located 240 km south of continental Australia. We sampled eagles in six different regions of Tasmania, which differ in their ecological communities and density of eagle nests (Fig. 1; see Appendix A for more details). Our study was focused on young wedge-tailed eagles during the post-fledging dependence period (PFDP), which is the period between fledging the nest and the onset of natal dispersal. Understanding habitat use during this life stage has immense conservation significance, both because of the low reproductive rates of the species (~60 % of nesting attempts result in failure; Forest Practices Authority, 2017) and the reported high mortality rates for young eagles in Tasmania (~50 %; Bell and Mooney, 1998).

2.2. Data collection

We attached GPS-GSM solar-powered telemetry units (CTT-1000-BT3 Series; Cellular Tracking Technologies, Rio Grande, NJ, USA) to nestling Tasmanian wedge-tailed eagles (see Appendix A for details on nestling selection and capture). Each telemetry unit weighed ~65 g (1.47–1.96 % of body mass) and was attached as a backpack using an 11.2 mm Teflon ribbon harness (Bally Ribbon Mills, Bally, PA). The telemetry units recorded GPS fixes every 15 min, from 1 h before sunrise to 1 h after sunset. The GPS calculated time of local sunrise and sunset, and so number of fixes varied throughout the year with day length. Movement data associated with each fix included location, altitude, speed, course over ground, and horizontal dilution of precision (HDOP). All fixes with a HDOP > 4 (9.7 % of raw data) were filtered from the final data set to maximize spatial accuracy.

2.3. Calculating duration of the post-fledging dependence period (PFDP)

To estimate the total length of the PFDP for each eagle we identified the fledging date (start of PFDP) and the initiation of natal dispersal (end of PFDP). Fledging was considered to have occurred when four consecutive GPS fixes were >10 m from the nest tree. We defined the onset of natal dispersal as the first day the bird travelled >7 km from the natal nest and subsequently was not <5 km from the nest for the following 10 days ('Method 7' from Weston et al., 2013). We did not include the first 50 days of the PFDP in the analysis, as during this period the young eagles were still associated with their natal nest, thus confounding how they selected habitats.

2.4. Data analysis

2.4.1. Identifying behavioral states

We classified the GPS fixes for each animal into movement states based on the distance and turning angles between consecutive GPS fixes using Hidden Markov Models (HMMs). HMM analyses are state-switching models that assume animal movement is driven by underlying behavioral modes (Patterson et al., 2017). We used HMMs (R package 'moveHMM'; Michelot et al., 2016) to estimate the probability of each GPS fix being in each of three hypothesized behavioral states (state 1: a stationary state; state 2: characterized by movements over shorter distances with variable turning angles; state 3: characterized by movements over longer distances with relatively constant turning angles), and we assigned each GPS fix the state with the highest probability. We included models using both step lengths and turning angles as well as models using solely step lengths. HMMs require the user defines the number of states and the initial parameters for each state. Following protocols in Michelot et al. (2016), we ran 100 model iterations each considering different initial parameters to establish the optimal parameters to delineate the behavioral states. We identified the best

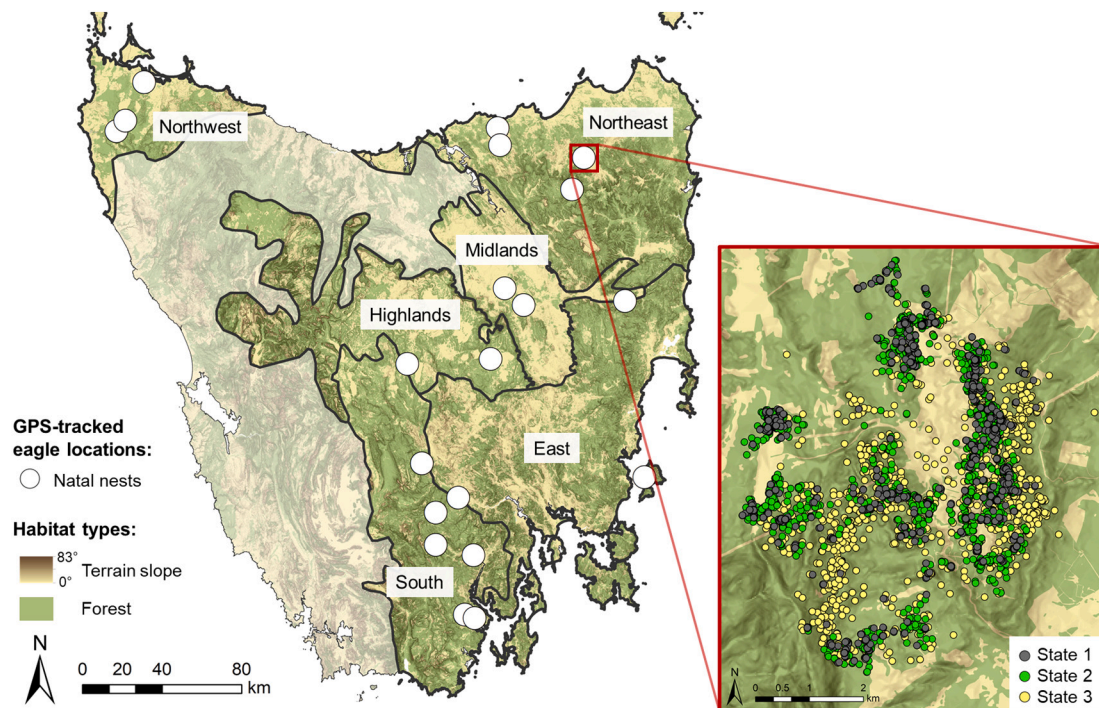


Fig. 1. Location of Tasmanian wedge-tailed eagle nest sites where nestlings were fitted with a GPS telemetry unit during 2017 and 2018. At two of these nests, a nestling was fitted with a GPS transmitter in both the 2017 and 2018 breeding seasons. The regions used to compare model performance in different areas of Tasmania are labelled, with slope and forest cover indicated by the shade of the land area. Inset shows the GPS location from one of the eagles, colored by behavioral state: state 1 (perching), state 2 (short flights) and state 3 (long flights).

performing model by comparing the hessian matrices, state transition confidence intervals, state step length and turning angle distributions, and AIC.

2.4.2. Associating behavioral states with habitats

Once all GPS fixes had been assigned to a state, we used behavior-specific variograms (function ‘variogram’ in R package ‘ctmm’; Calabrese et al., 2016) to visualize the data for each individual and to identify a time threshold in which variance stabilized and each location could be considered independent. For each behavioral state, we then subsampled the GPS data by the time threshold specific to that state (function ‘track_resample’ in R package ‘amt’; Signer et al., 2019) before calculating univariate habitat selection ratios (Manly et al., 2002; function ‘widesIII’ in R package ‘AdehabitatHS’; Calenge, 2006). This approach compares the proportion of available habitat types to the proportion of time spent in each habitat. We defined the available habitat for each eagle by creating a 95 % minimum convex polygon (MCP) from the GPS data during the PFDP and buffering that area by an additional band that added 5 % to the total area of the MCP (Appendix B). The proportion of time spent performing each behavior in each habitat type was measured by the proportion of GPS fixes that fell within each habitat. The selection ratio (w_i) values identify which habitats are being selected. As such, $w_i < 1$ indicates a habitat used proportionally less than its availability (i.e., a w_i of 0.5 indicates a habitat type used half as often as expected), and $w_i > 1$ indicates a habitat used proportionally more than its availability (i.e., a w_i of 2 indicates a habitat type used twice as often as expected). The habitat features we considered were slope, aspect, terrain ruggedness, distance to nearest ridgeline, and distance to nearest forest edge (DPIPWE, 2013, 2010; for derivation of habitat variables see Appendix B). These were selected based on the ecology of the study species and published work on congeners (Appendix B). All habitat variables were delineated as raster files with a 30 m² resolution. We assigned each GPS fix the habitat values from the raster cell in which they were located (function ‘extract’ in R package ‘raster’; Hijmans et al., 2021). Due to the number of behavioral states and habitat

variables, we adopted a highly conservative significance level of $p = 0.001$ to reduce Type 1 error rates.

2.4.3. Predicting where different behaviors occur

We used a multivariate habitat selection ratio to predict where eagle behaviors are likely to occur (Basson et al., 2012; Eveson et al., 2015; Patterson et al., 2016). We chose this technique instead of a generalized linear model (GLM) based resource selection analysis (e.g., Fortin et al., 2005) because there is contention over how best to place the pseudo-absences that are often required for a GLM approach (e.g., VanDerWal et al., 2009).

We included habitat variables in the multivariate model that were identified as significant from the univariate habitat selection ratios (as calculated in Section 2.4.2, above). If habitat variables were spatially autocorrelated (Pearson’s $r > 0.8$; ‘layerStats’ function in R package ‘raster’; Hijmans et al., 2021), we retained the variable for which the eagles showed a stronger univariate selection (χ^2). We created a 30 m² raster stack of the habitat covariates and calculated, for each bird, both the available (from the buffered 95 % MCP) and used (extracted habitat values for each GPS fix) proportion of the combination of covariates. The Selection Value (SV) was then calculated as

$$SV = \left(\sum_{i=1}^n h(U)_i / h(A)_i \right) / n \quad (1)$$

where i represents each individual, n is the total number of individuals, $h(A)$ represents the joint frequency distribution of habitat covariates across the areas available to each individual, and $h(U)$ represents the joint frequency distribution of habitat covariates used by each individual (Patterson et al., 2016). The SV is therefore an averaged selection ratio across all individuals, which should give a population-level estimate better suited for predicting new activity (Matthiopoulos et al., 2020). The SV is interpreted similarly to the w_i habitat selection ratio (i.e., $SV > 1$ indicating selection, $SV < 1$ indicating avoidance). We constructed habitat selection maps as raster images for each behavior by

taking the relevant habitat covariate values for each 30 m² pixel and assigning the associated SV.

2.4.4. Cross-validation of behavior-specific spatial models

To evaluate the predictive performance of the behavior-specific SV models, we used methods proposed by Boyce et al. (2002) and Johnson et al. (2006) that we modified to include a leave-one-out cross-validation (LOOCV) framework. We used LOOCV instead of temporal or random *k*-fold partitioning, as our aim was to assess the predictive ability of the models for areas and individuals across Tasmania. We repeatedly ran the SV estimation for each model, in each case leaving out all GPS data from one individual, and then using those as test data for model validation (the number of repetitions of the SV estimation therefore was equal to the number of birds tagged). For each run of the LOOCV we calculated the SV for each 30 m² grid cell of available habitat for the test eagle. We reclassified the continuous SV values into six ordinal bins, ensuring validation points and reliable amounts of available land area in each bin. We then calculated the proportion of GPS fixes that were expected to fall within each SV bin based on the model (Eqs. (4) and (5) in Johnson et al., 2006) and compared this to the proportion of test data GPS fixes that fell within the corresponding bin. Model performance was assessed by comparing the expected and observed values using linear regression and Spearman-rank correlation. A model that predicts habitat use accurately would have a regression intercept (b_0) approaching 0, a regression slope (b_1) approaching 1 and significantly different from 0, a high regression R^2 value (good ≥ 0.8 , moderate = 0.5–0.8), and a significant positive rank correlation (Boyce et al., 2002; Johnson et al., 2006).

To explore spatial variability in model performance we grouped eagles according to the geographic regions and we calculated for each region the mean expected vs. observed regression R^2 values, the mean rank correlation r_s values, and the percentage of individual cross validation runs that the models predicted well according to all measures of model performance.

3. Results

We attached GPS telemetry units to 22 Tasmanian wedge-tailed eagle nestlings from 20 different natal territories during the 2016–2017 ($n = 7$) and 2017–2018 ($n = 15$) breeding seasons (a maximum of one bird per territory per year). Our data consisted of 231,478 GPS fixes, with a mean number of fixes per eagle of 10,522 (range: 5299–22,373). The grand mean 15-min step length was 263.4 m (per-individual mean range: 77–410.8 m), with the maximum step length by each individual ranging from 2456 to 7078 m (Appendix Table C.1). The mean duration of the PFDP was 331.4 ± 158 days (\pm SD; range 148–607; Appendix Table C.1). There was little variation in the duration of the PFDP between the two breeding seasons studied (2016–2017 season mean = 310 ± 170 days; 2017–2018 mean = 341 ± 151 days). The mean size of available habitat (buffered 95 % MCP) was 34.4 km² (range: 10.4–94.5 km²; Appendix Table C.1).

3.1. Identifying behavioral states

The best performing HMM differentiated the three behavioral states using only step length as follows: state 1, a stationary state characterized by very small movements had a mean step length of 10 ± 8 m (\pm SD), 41.8 % of GPS fixes (Appendix Table C.2); state 2 characterized by intermediate distance movements had a mean step length of 166 ± 96 m, 39.3 %; and state 3 characterized by relatively longer distance movements with a mean step length of 795 ± 414 m, 18.9 % (Appendix Table C.2 and Fig. C.1). Models including turning angle performed less well, with turning angle distributions varying little between the states 2 and 3 (Appendix Fig. C.2). Early (≤ 2 h after sunrise) and late (≤ 2 h before sunset) in the day, birds spent the highest proportion of their time in state 1 (61.1 % of GPS fixes during these 4 h). During the 3 h in the

middle of the day state 3 was the commonest behavior (34.2 % of GPS fixes; Appendix Fig. C.3).

3.2. Associating behavioral states with habitats

The variance of the GPS-data stabilized and the temporal autocorrelation decreased around 4 h for state 1, 2 h for state 2, and 1 h for state 3 (Appendix Fig. C.4). We therefore subsampled the GPS data by these behavior-specific time thresholds, leaving 33,176 GPS locations (state 1 = 9111; state 2 = 13,485; state 3 = 10,580).

The univariate habitat selection ratios suggested that eagles used habitats non-randomly in all three behavioral states ($p < 0.001$) with respect to distance from forest edge, terrain slope, and terrain ruggedness, but not with respect to distance to ridgeline or to aspect (Appendix Table C.3). Some of these patterns of selection were constant across all three states, others were not.

In all three behavioral states, selection was positive for areas < 25 m from the nearest forest edge (state 1 $w_i = 2.9$, state 2 $w_i = 2.9$, state 3 $w_i = 2.2$) and negative for open areas > 75 m from the nearest forest edge (state 1 $w_i = 0.1$ –0.4, state 2 $w_i = 0.1$ –0.4, state 3 $w_i = 0.2$ –0.5; Appendix Fig. C.5a). Selection was always positive ($w_i > 1$) for land with steeper slopes ($> 15^\circ$), and land with gentler slopes ($< 10^\circ$) was always either underused or used in proportion to its availability (Appendix Fig. C.5b). Likewise, eagles selected for more rugged terrain during all three behavioral states (Appendix Fig. C.6b).

Differences in selection among states were detected relative to distance from forest edge and terrain slope. Selection was negative for areas over forest and far (> 75 m) from the forest edge during state 1 ($w_i = 0.5$ –0.9) and state 2 ($w_i = 0.4$ –0.8), but eagles generally used those areas proportional to their availability ($w_i \approx 1$) during state 3 (Appendix Fig. C.5a). Finally, selection for areas with steeper slopes ($> 15^\circ$) was stronger for state 3 ($w_i = 1.6$ –2.4), and during state 3 eagles showed a slightly stronger avoidance of flatter (0 – 5°) terrain (Appendix Fig. C.5b).

3.3. Predicting where different behaviors occur

The habitat selection ratio analyses identified distance to forest edge, slope, and terrain ruggedness for inclusion in the multivariate predictive models. Ruggedness and slope were correlated (Pearson's $r = 0.91$), thus we excluded ruggedness from the final model because selection was slightly weaker for this parameter. The models showed that habitat selection during state 1 and state 2 was very similar, with eagles avoiding open areas (> 75 m from the nearest forest) regardless of topography and positively selecting for areas over the forest with very steep terrain ($> 20^\circ$; Fig. 2a and Fig. 2b). Therefore, although the univariate selection ratios suggested negative selection for areas over forest and far from the forest edge during states 1 and 2, the multivariate ratio indicates that the eagles selected positively for these areas if they occurred on steep slopes. During state 3 the eagles positively selected for areas further from the forest edges, especially areas over forests with a topographic slope $> 5^\circ$ (Fig. 2c).

The models showed that habitats that were utilized proportionally less than their availability ($SV < 1$) made up 60–64 % of the available land area, with 20–28 % of GPS fixes for the associated behavior in these areas. By contrast, 6–9 % of GPS fixes for each behavior occurred in areas assigned SVs > 4 , yet these habitats covered 1–2 % of the available land area (Appendix Table D.1).

3.4. Cross-validation of behavior-specific spatial models

LOOCV indicated good predictive performance of the behavioral models (regression: $b_0 = -0.018$ –0.000, $b_1 = 0.971$ –1.110, $R^2 = 0.929$ –0.975; rank correlation: $r_s = 0.943$ –1.000, $p = 0.003$ –0.017; Fig. 3; Appendix Figs. D.1, D.2, and D.3). However, model performance varied among regions (Table 1, Appendix D). The state 1 model performed well in the East, Highlands, and Northeast ($R^2 > 0.8$; $r_s > 0.8$),

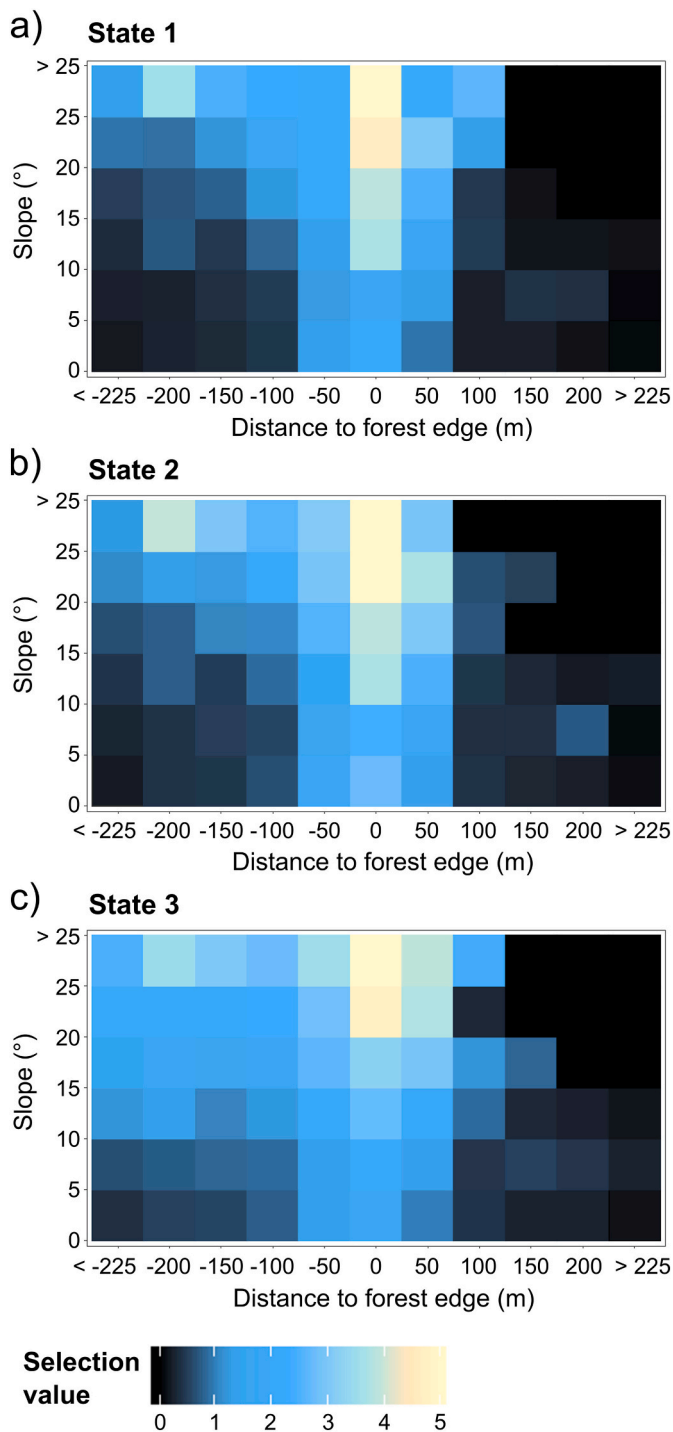


Fig. 2. Bivariate habitat selection surfaces for young Tasmanian wedge-tailed eagles according to the slope of the terrain and the distance to nearest forest edge (negative forest edge values are inside the forest; positive values are outside the forest). Each surface summarizes habitat selection during a specific behavioral state: (a) state 1: perching, (b) state 2: short flights and (c) state 3: long flights. The color scale specifies the selection values (SVs) for the corresponding combinations of habitat types. Selection values <1 indicate habitats used proportionally less than their availability in the landscape.

but had only moderate predictive ability in the Midlands, Northwest, and South ($R^2 = 0.4\text{--}0.8$). Furthermore, the state 1 model only performed well according to all measures of model performance for >50 % of individual cross validation runs for the East region. The state 2 model performed well in the Northeast, East, South, and Highlands ($R^2 > 0.9$;

$r_s > 0.8$), but poorly in the Midlands and Northwest ($R^2 = 0.3\text{--}0.4$). The state 3 model had high predictive ability across all regions ($R^2 > 0.9$; $r_s > 0.9$).

4. Discussion

This study shows how behavior-specific habitat selection analyses can provide insight into how species use resources for different behaviors. Our approach provides a template for spatially explicit predictions of where different behaviors are likely to occur, as well as for assessment of the predictive capacity of spatial models. Using these methods, we provide the first quantitative assessment of behavior-specific habitat-use by the wedge-tailed eagle anywhere in its range. These findings have important implications for our understanding of the ecology of the Tasmanian wedge-tailed eagle and for the management of this endangered population in the face of increasing land use changes.

4.1. Identifying behavioral states

We were able to characterize three statistically defined behavioral states in the Tasmanian wedge-tailed eagle GPS-tracking data. Care should be taken to not over-interpret the biological meaning of the behavioral states identified (Patterson et al., 2009), as an animal may have multiple underlying motivations for a single statistically characterized behavioral state. Likewise, the temporal resolution of GPS fixes may mean that an individual can exhibit several different behaviors within each interval. We therefore interpret the three behavioral states based on the descriptive statistics of each state and our understanding of the ecology of the species.

State 1 likely consisted of perching or roosting behavior, as step lengths were approximately within the locational measurement error of the GPS units, indicating that the birds were predominantly stationary or moving only a few meters at a time (e.g., walking, not flying). This interpretation is substantiated by post hoc analysis showing that state 1 occurred at low altitudes ($\bar{x} = 20.6 \pm 5.3$ m; \pm SD; flight altitude calculated as in Poessel et al., 2018b) and that this state was more common at the beginning and end of the day, when birds are likely to be at roost sites. As well as resting, state 1 also likely comprises behaviors such as prey handling and foraging, as wedge-tailed eagles commonly hunt from perch vantage points (Olsen, 2005). Both states 2 and 3 involved transitory movements around the natal territory and behaviors such as soaring and hunting from the wing. We interpret state 2 as short, low flights that are likely to involve flapping-gliding behaviors, since they were shorter in duration and occurred at much lower altitudes ($\bar{x} = 22.8 \pm 5.9$ m; Sapir et al., 2011; Sur et al., 2021). State 3, which was characterized by high flight altitudes ($\bar{x} = 63.5 \pm 23.6$ m) and longer step lengths, is indicative of longer flights involving soaring behavior. The circadian patterns in State 3 are also consistent with this interpretation, as state 3 was most common in the middle of the day when the thermal updrafts used by soaring birds are strongest (Poessel et al., 2018a).

4.2. Associating behavioral states with habitats

Young eagles showed strong selection for forest edges when perching and performing short flights. This is probably due both to the high habitat suitability for foraging in these ecotones and to the safety provided by forests for these inexperienced fliers. Forest edges are primary foraging habitats for many predatory species, including other *Aquila* spp. (Balbontin, 2005), as they provide expansive views, access to spatially open habitats conducive to hunting, and often have higher densities of prey species. Likewise, the cover provided to young eagles by these habitats likely provides some protection from predators including other eagles and humans.

We observed strong positive selection for steeper slopes by eagles performing long flights, a pattern consistent with data from congeners

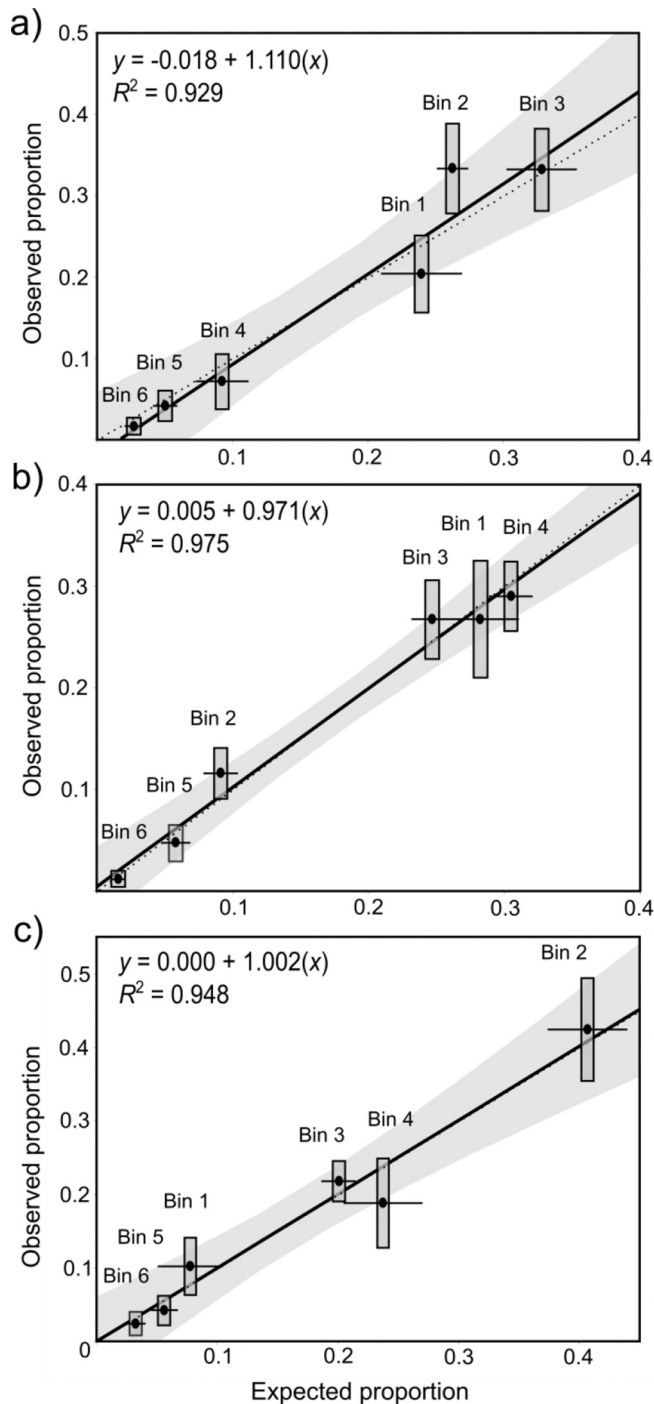


Fig. 3. Expected vs. observed regressions assessing performance of the models for each behavioral state: (a) state 1: perching, (b) state 2: short flights and (c) state 3: long flights. The observed proportion is the proportion of GPS fixes in six SV bins for each of 22 leave-one-out cross-validated (LOOCV) runs. The expected proportion is the proportion of cross-validated GPS fixes that were expected to fall within each SV bin based on the model prediction. The averaged performance of each bin is plotted, with the vertical error bars designating the observed proportion 95 % CI and the horizontal lines the 95 % CI of the expected proportion. The fitted regression of the LOOCV performance of each bin is shown as the solid dark line, with the shaded gray area denoting the 95 % CI. A model 100 % accurate in predicting habitat use would have a regression line with a small CI that sat along the dashed line.

and other soaring species (Katzner et al., 2012; Poessel et al., 2018a; Tikkanen et al., 2018). Steeper topography and more variable terrain facilitate orographic updrafts, which can be exploited during flight for the vertical air movements they provide (Duerr et al., 2012; Fielding et al., 2019; Newton, 2008). As such, our findings of a stronger selection for steep slopes during long flights suggest that orographic winds are important to this behavior.

The consistency of our results with the general understanding of the species' natural history indicates our results are robust to the limitations of the habitat selection ratio method we used. Selection ratios require that GPS locations are separated by sufficient time to be considered independent, as otherwise an individual will be selecting from a pool of habitats smaller than the defined available area. Therefore, employing a method to sub-sample the locations to ensure spatial independence, such as the behavior-specific variograms we use, is important to addressing this constraint. Furthermore, considering available habitat at the home range level assumes that an animal can move throughout their home range between observations. This makes the approach we used well suited to animals that can move across their home range within a short time period, but less appropriate for transitory animals (e.g., dispersing or nomadic individuals) or animals with very large home ranges.

4.3. Cross-validation of behavior-specific spatial models

The validation of maps produced by habitat-use models is often neglected, despite the widespread application of such maps for conservation management (Johnson et al., 2006). Furthermore, few studies assess regional differences in performance of habitat-use models, with predictions typically generalized across an entire study area. For soaring birds, this runs contrary to recent evidence that movement behavior is regionally variable (Duerr et al., 2019; Sur et al., 2020). Our study builds on those findings, as our behavior-specific habitat-use models varied in predictive performance with behavior and across regions. The model for perching (state 1) performed least well, with only moderate cross-validated performance in most regions of Tasmania. Although the eagles generally selected steep areas at the forest edge for perching, paddock trees are also important perching habitats for the species. These isolated trees are not detected effectively in our landcover dataset, which may explain the limited ability of the model to accurately predict perching areas. The models using distance to forest edge and topographic slope predicted the location of flying behaviors with more accuracy, and these variables were effectively characterized by our landcover and topographic input data. The long flight (state 3) model had high predictive accuracy across all regions, whereas the short flight (state 2) model performed well except in the Northwest and Midlands. In these flatter landscapes the eagles selected more strongly for forest edges (Appendix E), suggesting models localized to these regions would more effectively predict where short flights occur. Together, these patterns thus emphasize the importance of cross validation for validation of spatially explicit habitat selection models.

4.4. Conservation applications

Our behavior-specific habitat selection analyses provide valuable new insights to guide the conservation management of the Tasmanian wedge-tailed eagle. The young birds we considered avoided large open areas, suggesting that forest managers may improve the habitat quality for this life stage by retaining and restoring patches of standing forest in areas that have been harvested or cleared (Lindenmayer et al., 2012). Similarly, the habitat selection models for flying behaviors can be used to guide efforts to reduce risks from sources of human-caused mortality. Short flights occurred at low altitudes that overlap the heights of power line poles in the state (12–50 m; TasNetworks pers. comm.). Our predictive mapping of state 2 behaviors can therefore guide prioritization of high-risk areas for mitigation and positioning of future infrastructure. For example, flight diverters on power lines (Bernardino et al., 2018)

Table 1

Regional summaries of the leave-one-out cross-validated (LOOCV) performance for spatial models predicting where young Tasmanian wedge-tailed eagles exhibit each of three behavioral states (state 1: perching; state 2: short flights; state 3: long flights). The mean expected vs. observed regression R^2 values, the mean Spearman's rank correlation r_s , and the percentage of individual cross validation runs that predicted well according to all measures of model performance are presented.

Region	State 1 model			State 2 model			State 3 model		
	R^2	r_s	%	R^2	r_s	%	R^2	r_s	%
East	0.966	0.971	100	0.932	0.886	50	0.972	0.935	100
Highlands	0.964	0.886	50	0.9	0.857	50	0.989	0.914	50
Midlands	0.427	0.803	0	0.343	0.634	0	0.931	0.913	100
Northeast	0.864	0.857	50	0.902	0.996	75	0.962	0.968	100
Northwest	0.517	0.871	33	0.378	0.899	33	0.943	0.952	100
South	0.796	0.927	25	0.846	0.907	75	0.907	0.9	75
All animals	0.929	0.943	36.4	0.975	1	54.5	0.948	0.943	86.4

closer than 75 m from forest might be relatively more useful than on power lines farther from forests. Additionally, long flights occurred at higher altitudes that may be associated with higher risk of wind turbine collision (rotor swept areas of turbines in Tasmania range 30–170 m above ground; [Cattle Hill Wind Farm, 2021](#); [Hydro-Electric Corporation, 2019](#)). With Tasmania's landscape being increasingly exploited for wind energy projects, the state 3 model may prove a useful first step in estimating risk to birds.

There are important provisos to the application of our behavior specific habitat selection models as conservation management tools. First, the models are specific to the habitats used by wedge-tailed eagles during the post-fledging dependence period. Thus, the predictions from these models are specific to eagles during this life-stage and localized to areas that support a breeding territory. The models could most effectively be used in conjunction with state-wide estimations of nesting habitat suitability ([Koch et al., 2013](#)) or known nest sites ([DPIPWE, 2016](#)). Second, predictive ability of these models is likely limited in regions with lower cross-validated performance or with an absence of eagle tracking data (e.g., regions of expansive buttongrass, *Gymnoschoenus sphaerocephalus*, moorlands characteristic of west and south-west Tasmania; [DPIPWE, 2013](#)).

4.5. Conclusion

Habitat selection models only rarely account for behavior. Our study provides a framework for spatially explicit and behavior-specific habitat selection analyses that can be applied to other species of conservation concern. We used a methodological approach based on selection ratios to explore how different resources are used for different behaviors and to predict where these behaviors are likely to occur across the landscape. Further, our inclusion of leave-one-out cross-validation allowed the predictive ability of models to be broken down at different scales of inference. This ensures that only high-performing models are passed on to conservation managers. In the case of the Tasmanian wedge-tailed eagle, this framework has provided important insights into behavior-specific habitat associations that have direct conservation relevance.

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CRedit authorship contribution statement

James M. Pay: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Project administration, Funding acquisition. **Toby A. Patterson:** Methodology, Formal analysis, Writing – review & editing. **Kirstin M. Proft:**

Methodology, Formal analysis, Writing – review & editing. **Elissa Z. Cameron:** Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Clare E. Hawkins:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition. **Amelia J. Koch:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition. **Jason M. Wiersma:** Conceptualization, Investigation, Writing – review & editing. **Todd E. Katzner:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Disclaimer

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Data accessibility

Data, associated metadata, and calculation tools are available from the corresponding author.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109743>.

References

- Abrahams, B., Jordan, N.R., Golabek, K.A., McNutt, J.W., Wilson, A.M., Brashares, J.S., 2016. Lessons from integrating behaviour and resource selection: activity-specific responses of african wild dogs to roads. *Anim. Conserv.* 19, 247–255. <https://doi.org/10.1111/acv.12235>.
- Balbotín, J., 2005. Identifying suitable habitat for dispersal in Bonelli's eagle: an important issue in halting its decline in Europe. *Biol. Conserv.* 126, 74–83. <https://doi.org/10.1016/j.biocon.2005.04.023>.
- Basson, M., Hobday, A.J., Eveson, J.P., Patterson, T., 2012. Spatial Interactions Among Juvenile Southern Bluefin Tuna at the Global Scale: A Large Scale Archival Tag Experiment. FRDC Rep. 2003/002.
- Bekessy, S.A., Wintle, B.A., Gordon, A., Fox, J.C., Chisholm, R., Brown, B., Regan, T., Mooney, N., Read, S.M., Burgman, M.A., 2009. Modelling human impacts on the tasmanian wedge-tailed eagle (*Aquila audax fleayi*). *Biol. Conserv.* 142, 2438–2448. <https://doi.org/10.1016/j.biocon.2009.05.010>.
- Bell, P., Mooney, N., 1998. Wedge-tailed Eagle Recovery Plan 1998–2003. Department of Primary Industries, Parks, Water and Environment, Hobart.
- Bernardino, J., Bevanger, K., Barrientos, R., Dwyer, J.F., Marques, A.T., Martins, R.C., Shaw, J.M., Silva, J.P., Moreira, F., 2018. Bird collisions with power lines: state of the art and priority areas for research. *Biol. Conserv.* 222, 1–13. <https://doi.org/10.1016/j.biocon.2018.02.029>.
- Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R.C., Odden, J., Linnell, J.D.C., 2015. Eurasian lynx habitat selection in human-modified landscape in Norway: effects of different human habitat modifications and behavioral states. *Biol. Conserv.* 191, 291–299. <https://doi.org/10.1016/j.biocon.2015.07.007>.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Model.* 157, 281–300. [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4).
- Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. Ctm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* 7, 1124–1132.
- Calenge, C., 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>.
- Cattle Hill Wind Farm, 2021. Cattle hill wind farm overview [WWW document]. URL. <https://cattlehillwindfarm.com/project/>. (Accessed 28 October 2021).
- Commonwealth of Australia, 1999. Environment Protection and Biodiversity Conservation Act 1999 - EPBC Act List of Threatened Fauna. Canberra.
- DPIPWE, 2010. Tasmania 25 Metre Digital Elevation Model, 3rd edition. Land Tasmania, Hobart.
- DPIPWE, 2013. TASVEG 3.0. Tasmanian Vegetation Monitoring and Mapping Program, Hobart.
- DPIPWE, 2016. Natural values atlas, Tasmania [WWW document]. URL. <https://www.naturalvaluesatlas.tas.gov.au/>. (Accessed 8 July 2019).
- Duerr, A.E., Miller, T., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K., Maisonneuve, C., Tremblay, J., Katzner, T.E., 2012. Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. *PLoS One* 7, e35548. <https://doi.org/10.1371/journal.pone.0035548>.
- Duerr, A.E., Miller, T.A., Dunn, L., Bell, D.A., Bloom, P.H., Fisher, R.N., Tracey, J.A., Katzner, T.E., 2019. Topographic drivers of flight altitude over large spatial and temporal scales. *Auk* 136, 1–11. <https://doi.org/10.1093/auk/ukz002>.
- Eveson, J.P., Hobday, A.J., Hartog, J.R., Spillman, C.M., Rough, K.M., 2015. Seasonal forecasting of tuna habitat in the great australian bight. *Fish. Res.* 170, 39–49. <https://doi.org/10.1016/j.fishres.2015.05.008>.
- Fielding, A.H., Haworth, P.F., Anderson, D., Benn, S., Dennis, R., Weston, E., Whitfield, D.P., 2019. A simple topographical model to predict golden eagle *Aquila chrysaetos* space use during dispersal. *Ibis (Lond. 1859)* 162, 400–415. <https://doi.org/10.1111/ibi.12718>.
- Forest Practices Authority, 2017. Monitoring the Effectiveness of the Biodiversity Provisions of the Tasmanian Forest Practices Code: 2016–17 Summary Report. Forest Practices Authority, Hobart.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Mao, J.S., Ecology, S., May, N., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in yellowstone National Park. *Ecology* 86, 1320–1330.
- Garnet, S., Baker, B.G., 2020. The Action Plan for Australian Birds. CSIRO Publishing, Clayton South.
- Hijmans, R.J., van Etten, J., Sumner, M., Cheng, J., Bevan, A., Bivand, R., Busetto, L., Canty, M., Forrester, D., Ghosh, A., Golicher, D., Gray, J., Grrenbert, J.A., Hiemstra, P., 2021. raster: Geographic Data Analysis and Modeling. R Package Version 3.5-2.
- Hydro-Electric Corporation, 2019. Our power stations [WWW document]. URL. <https://www.hydro.com.au/clean-energy/our-power-stations/wind-power>. (Accessed 5 July 2019).
- Johnson, C.J., Seip, D.R., Boyce, M.S., 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *J. Appl. Ecol.* 41, 238–251. <https://doi.org/10.1111/j.0021-8901.2004.00899.x>.
- Johnson, C.J., Nielson, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *J. Wildl. Manag.* 70, 347–357. [https://doi.org/10.2193/0022-541x\(2006\)70\[347:rsfbou\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[347:rsfbou]2.0.co;2).
- Katzner, T.E., Brandes, D., Miller, T., Lanzone, M., Maisonneuve, C., Tremblay, J.A., Mulvihill, R., Merovich, G.T., 2012. Topography drives migratory flight altitude of golden eagles: implications for on-shore wind energy development. *J. Appl. Ecol.* 49, 1178–1186. <https://doi.org/10.1111/j.1365-2664.2012.02185.x>.
- Klar, N., Fernandez, N., Kramer-schadt, S., Herrmann, M., Trinzen, M., Buttner, I., Niemitz, C., 2008. Habitat selection models for european wildcat conservation. *Biol. Conserv.* 141, 308–319. <https://doi.org/10.1016/j.biocon.2007.10.004>.
- Koch, A.J., Wiersma, J.M., Munks, S.A., 2013. Tasmanian Wedge-tailed Eagle Nest Monitoring Project 2007–12: Nest Site Use, Timing of Breeding, and a Review of the Nesting Habitat Model. Forest Practices Authority, Hobart.
- Leroux, S.J., Schmiegelow, F.K.A., Cumming, S.G., Lessard, R.B., Nagy, J., 2007. Accounting for system dynamics in reserve design. *Ecol. Appl.* 17, 1954–1966.
- Lindenmayer, D.B., Franklin, J.F., Lohmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* 5, 421–431. <https://doi.org/10.1111/j.1755-263X.2012.00257.x>.
- Mahoney, P.J., Young, J.K., 2017. Uncovering behavioural states from animal activity and site fidelity patterns. *Methods Ecol. Evol.* 8, 174–183. <https://doi.org/10.1111/2041-210X.12658>.
- Manly, B., McDonald, L., Thomas, D., MacDonald, T., Erickson, W., 2002. Resource Selection by Animals. Statistical Design and Analysis for Field Studies. Kluwer Academic Publisher, Dordrecht.
- Matthiopoulos, J., Fieberg, J.R., Aarts, G., 2020. Species-Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights. University of Minnesota Libraries Publishing, Minneapolis–Saint Paul.
- Meisingset, E.L., Loe, L.E., Brekkum, O., Myrsterud, A., 2014. Targeting mitigation efforts: the role of speed limit and road edge clearance for deer-vehicle collisions. *J. Wildl. Manag.* 78, 679–688. <https://doi.org/10.1002/jwm.712>.
- Michelot, T.T., Langrock, R., Patterson, T.A., 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods Ecol. Evol.* 7, 1308–1315. <https://doi.org/10.1111/2041-210X.1257>.
- Miller, T., Brooks, R., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K., Maisonneuve, C., Tremblay, J., Duerr, A., Katzner, T., 2014. Assessing risk to birds from industrial wind energy development via paired resource selection models. *Conserv. Biol.* 28, 745–755. <https://doi.org/10.1111/cobi.12227>.
- Mooney, N., Holdsworth, M., 1991. The effects of disturbance on nesting wedge-tailed eagles (*Aquila audax fleayi*) in Tasmania. *Tasforests* 3, 15–31.
- Morales, J.M., Ellner, S.P., 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. *Ecology* 83, 2240–2247.
- Newton, I., 2008. The Migration Ecology of Birds. Academic Press, London.
- Olsen, P., 2005. Wedge-Tailed Eagle. CSIRO Publishing, Collingwood.
- Patterson, T.A., Basson, M., Bravington, M.V., Gunn, J.S., 2009. Classifying movement behaviour in relation to environmental conditions using hidden markov models. *J. Anim. Ecol.* 78, 1113–1123. <https://doi.org/10.1111/j.1365-2656.2009.01583.x>.
- Patterson, T.A., Sharples, R.J., Raymond, B., Welsford, D.C., Andrews-Goff, V., Lea, M.A., Goldworthy, S.D., Gales, N.J., Hindell, M., 2016. Foraging distribution overlap and marine reserve usage amongst sub-Antarctic predators inferred from a multi-species satellite tagging experiment. *Ecol. Indic.* 70, 531–544. <https://doi.org/10.1016/j.ecolind.2016.05.049>.
- Patterson, T.A., Parton, A., Langrock, R., Blackwell, P.G., Thomas, L., King, R., 2017. Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *AStA Adv. Stat. Anal.* 101, 399–438. <https://doi.org/10.1007/s10182-017-0302-7>.
- Pay, J.M., Katzner, T.E., Hawkins, C.E., Koch, A.J., Wiersma, J.M., Brown, W.E., Mooney, N.J., Cameron, E.Z., 2020. High frequency of lead exposure in the population of an endangered top predator, the tasmanian wedge-tailed eagle (*Aquila audax fleayi*). *Environ. Toxicol. Chem.* 40, 219–230.
- Pay, J.M., Katzner, T.E., Hawkins, C.E., Barmuta, L.A., Brown, W.E., Wiersma, J.M., Koch, A.J., Mooney, N.J., Cameron, E.Z., 2021. Endangered Australian top predator is frequently exposed to anticoagulant rodenticides. *Sci. Total Environ.* 788, 147673 <https://doi.org/10.1016/j.scitotenv.2021.147673>.
- Poessel, S.A., Brandt, J., Miller, T.A., Katzner, T.E., 2018. Meteorological and environmental variables affect flight behaviour and decision-making of an obligate soaring bird, the California condor *Gymnogyps californianus*. *Ibis (Lond. 1859)* 160, 36–53. <https://doi.org/10.1111/ibi.12531>.
- Poessel, S.A., Duerr, A.E., Hall, J.C., Braham, M.A., Katzner, T.E., 2018b. Improving estimation of flight altitude in wildlife telemetry studies. *J. Appl. Ecol.* 55, 2064–2070. <https://doi.org/10.1111/1365-2664.13135>.
- Reid, T., Krüger, S., Whitfield, D.P., Amar, A., 2015. Using spatial analyses of bearded vulture movements in southern Africa to inform wind turbine placement. *J. Appl. Ecol.* 52, 881–892. <https://doi.org/10.1111/1365-2664.12468>.
- Roeber, C.L., Beyer, H.L., Chase, M.J., Van Aarde, R.J., 2014. The pitfalls of ignoring behaviour when quantifying habitat selection. *Divers. Distrib.* 20, 322–333. <https://doi.org/10.1111/ddi.12164>.
- Sapir, N., Horvitz, N., Wikelski, M., Avissar, R., Mahrer, Y., Nathan, R., 2011. Migration by soaring or flapping: numerical atmospheric simulations reveal that turbulence kinetic energy dictates bee-eater flight mode. *Proc. R. Soc. B Biol. Sci.* 278, 3380–3386. <https://doi.org/10.1098/rspb.2011.0358>.
- Sawyer, H., Nielson, R.M., Lindzey, F., McDonald, L.L., 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *J. Wildl. Manag.* 70, 396–403.

- Seip, D.R., Columbia, B., Service, F., George, P., VI, B.C., 2007. Displacement of mountain caribou from winter habitat by snowmobiles. *J. Wildl. Manag.* 71, 1539–1544. <https://doi.org/10.2193/2006-387>.
- Signer, J., Fieberg, J., Avgar, T., 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.* 9, 880–890. <https://doi.org/10.1002/ece3.4823>.
- Sur, M., Duerr, A.E., Bell, D.A., Fisher, R.N., Tracey, J.A., Bloom, P.H., Miller, T.A., Katzner, T.E., 2020. Relevance of individual and environmental drivers of movement of Golden Eagles. *Ibis (Lond. 1859)* 162, 381–399. <https://doi.org/10.1111/ibi.12766>.
- Sur, M., Woodbridge, B., Esque, T.C., Belthoff, J.R., Bloom, P.H., Fisher, R.N., Longshore, K., Nussear, K.E., Tracey, J.A., Braham, M.A., Katzner, T.E., 2021. Linking behavioral states to landscape features for improved conservation management. *Ecol. Evol.* 11, 7905–7916. <https://doi.org/10.1002/ece3.7621>.
- Threatened Species Section, 2006. *Threatened Tasmanian Eagles Recovery Plan: 2006–2010*. Department of Primary Industries, Parks, Water and Environment, Hobart.
- Thurfjell, H., Ciuti, S., Boyce, M.S., 2014. Applications of step-selection functions in ecology and conservation. *Mov. Ecol.* 2, 4.
- Tikkanen, H., Rytönen, S., Karlin, O.P., Ollila, T., Pakanen, V.M., Tuohimaa, H., Orell, M., 2018. Modelling golden eagle habitat selection and flight activity in their home ranges for safer wind farm planning. *Environ. Impact Assess. Rev.* 71, 120–131. <https://doi.org/10.1016/j.eiar.2018.04.006>.
- VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Model.* 220, 589–594. <https://doi.org/10.1016/j.ecolmodel.2008.11.010>.
- Weston, E.D., Whitfield, D.P., Travis, J.M.J., Lambin, X., 2013. When do young birds disperse? Tests from studies of golden eagles in Scotland. *BMC Ecol.* 13, 42. <https://doi.org/10.1186/1472-6785-13-42>.