A SPATIALLY EXPLICIT HABITAT SELECTION MODEL INCORPORATING HOME RANGE BEHAVIOR

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Abstract. Understanding habitat selection is of primary interest in theoretical and applied ecology. One approach is to infer habitat selection processes from differences in population densities between habitats using methods such as isodar and isoleg analysis. Another approach is to directly observe the movements of individuals. However, habitat selection models based on movement data often fail to adequately incorporate spatial processes. This is problematic if the probability of selecting a particular habitat is dependent upon its spatial context. This would occur, for example, where organisms exhibit home range behavior and the choice of habitat is dependent on its location relative to the home range. In this paper we present a spatially explicit habitat selection model for movement data that incorporates home range behavior as a spatial process. Our approach extends a previous model by formulating the probability of selecting a habitat as a function of its distance from the animal's current location and home range center. We demonstrate that these enhancements lead to more parsimonious models when applied to a koala radio-tracking data set from eastern Australia. This approach could also be applied to modeling other spatial habitat selection processes, leading to more biologically meaningful models for a range of species and applications.

Key words: eastern Australia; habitat availability; habitat selection; home range; koala; movement; Phascolarctos cinereus; *radio-tracking; spatial processes; spatially explicit model.*

INTRODUCTION

Habitat selection is the process whereby individuals preferentially use a nonrandom set of available habitats (Morris 2003). These processes result from habitat-specific differences in fitness and have important implications for population dynamics (Fretwell and Lucas 1970, Holt 1985, Pulliam 1988). Inferences about habitat selection processes can be made indirectly from relative population densities in different habitats using isodar and isoleg analysis (Rosenzweig 1981, Morris 2003). A complementary, and arguably superior, approach is to directly observe the movement processes of individuals. These data are more difficult to obtain than relative densities and this is one of the reasons why there was a need to develop isodar and isoleg theory in the first place. However, technological advances for tracking individuals have made this an increasingly more viable option. The analysis of movement data for modeling habitat selection is therefore an active area of current research in theoretical and applied ecology (e.g., Arthur et al. 1996, Hjermann 2000).

Under the ideal free distribution, individuals select habitats freely and without cost (Fretwell and Lucas

1970). In this case, the spatial location of habitat is irrelevant because there are no costs or constraints to selecting habitat, regardless of where it is. In reality, this assumption is false because there are usually costs or constraints associated with moving to another location (Morris 1987). Therefore, the probability that an individual selects a habitat patch is likely to be dependent, not only on habitat type, but also on its spatial context. There are at least four spatial properties that may impact on this probability. These are the location of the habitat patch relative to: (1) the individual's current location, (2) the individual's home range, (3) competitors/predators, and (4) other habitat patches. Accounting for these processes in habitat selection models requires a spatially explicit approach.

Commonly used habitat selection models for movement data partially account for spatial processes by defining an area of available habitat as a subset of the entire landscape (e.g., Chamberlain et al. 2003). In these cases, a distinction is made between the spatial location of available and unavailable habitat. However, the choice of available habitat can be somewhat arbitrary (Aebischer et al. 1993). This is a limitation because the definition of available habitat has important implications for estimates of habitat selection parameters and model predictions (Johnson 1980). A further limitation is that the probability of selecting a habitat from within the available habitat area is not usually considered to be dependent on the individual's current

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location. Arthur et al. (1996) and Hjermann (2000) recently developed models in which habitat availability was explicitly dependent upon the individual's current location, but they did not model other spatial processes, such as home range behavior.

Arthur et al. (1996) assumed a circular window of equally available habitat around the individual's current location, from which a discrete choice of habitat is made in a fixed time interval. Habitat located outside this window was assumed to be unavailable. However, movement data often show higher frequencies of short moves than long moves (MacDiarmid et al. 1991, Hill et al. 1996, Roslin 2000), rather than the distribution of movement distances implied by this model. Hjermann (2000) used a continuous function of availability to account for individuals that move more or less continuously. However, in order to allow for differences in the duration between recorded locations, this model relies on several assumptions of random and correlated random walks on percolation clusters (Orbach 1986, Johnson et al. 1992). These assumptions may break down in real landscapes, particularly when movements are correlated due to home range behavior. In fact, the models of Arthur et al. (1996) and Hjermann (2000) were developed specifically for species that do not exhibit well-defined home ranges.

In this paper we extend the model developed by Arthur et al. (1996) to species that occupy home ranges. This is achieved by using a spatially explicit approach, whereby the probability of selecting a habitat is dependent upon the location of the individual's home range. In addition, we compare models that incorporate the circular window of availability of Arthur et al. (1996) with models that assume, in the absence of habitat selection, negative exponentially distributed movement distances. As an example, we apply our approach to a koala (*Phascolarctos cinereus*) radio-tracking data set from eastern Australia.

METHODS

Model formulation

Arthur et al. (1996) modeled the probability of observing the selection of a given habitat type. We modified this approach by modeling the probability of observing the selection of a given location instead. This allowed us to introduce spatial covariates, upon which habitat preference parameters depend.

We considered an individual making discrete movements, in a fixed time interval, on a landscape consisting of $j = 1, \ldots, n$ habitat types, and we defined the probability of a move from location a to b as

$$\Pr(a \text{ to } b) = \frac{\phi(a, b) \sum_{j=1}^{n} w_j I(b, j)}{\sum_{j=1}^{n} w_j \int_{I(c,j)=1} \phi(a, c) \, dc}. \quad (1)$$

Here $\phi(a, b)$ (similarly for $\phi(a, c)$) is the probability,

in the absence of habitat selection, of moving from location a to location b (hereafter referred to as the habitat-independent movement probability function); w_j is the habitat preference parameter for habitat j; $I(b, j)$ [similarly for $I(c,j)$] is an indicator function that equals 1 if the habitat at location b is of type j and equals 0, otherwise; c is any location in the landscape, and the integral is over all locations in the landscape of habitat type j. The denominator acts as a normalization constant. The habitat-independent movement probability function is similar in interpretation to the proportional availability of each habitat in the availability radius model of Arthur et al. (1996) and Hjermann's (2000) continuous availability function. Although $\phi(\ )$ can be thought of as a measure of the relative availability of habitat at a particular location, it seems more intuitive to think of it as the probability of moving to a location in the absence of habitat selection. The parameter w_j is a measure of the relative preference for habitat j, relative to all other habitats. If the w_js are standardized to sum to 1, they represent the probability of selecting habitat j, given that all habitats are equally available (Manly 1974).

In complex landscapes, the integral in Eq. 1 often will be analytically intractable. As an approximation, we assumed that the landscape consisted of $k = 1, \ldots, m$ discrete grid cells, each of a defined habitat type j, and then

$$\Pr(a \text{ to } b) \approx \frac{\phi(a, b) \sum_{j=1}^{n} w_j I(b, j)}{A \sum_{j=1}^{n} w_j \sum_{k=1}^{m} \phi(a, c_k) I(c_k, j)} \quad (2)$$

where A is the area of each grid cell, and c_k is the location of the center of grid cell k. In practice, we only calculated the denominator out to a distance from location a where the probability density became sufficiently low, rather than across the entire landscape (sensu Hjermann 2000).

For a data set consisting of $i = 1, \ldots, N$ pairs of independent, identically distributed, movements, it follows that the likelihood of the data, ℓ, given the model in Eq. 2, is

$$\ell = \prod_{i=1}^{N} \frac{\phi(a_i, b_i) \sum_{j=1}^{n} w_j I(b_i, j)}{A \sum_{j=1}^{n} w_j \sum_{k=1}^{m} \phi(a_i, c_k) I(c_k, j)}. \quad (3)$$

Here a_i is the starting location for move i, and b_i is the location arrived at for move i.

We chose, a priori, two alternative habitat-independent movement probability functions, which were: (1) an availability radius, making the model a spatially explicit version of the model of Arthur et al. (1996) (see Appendix A), and (2) specified by a negative-exponential distribution of habitat-independent move-

ment distances. Hereafter, we refer to these models as the availability radius model and the negative-exponential model, respectively. The availability radius model assumes that all locations within a given radius are equally available (sensu Arthur et al. 1996). This implies that the costs or constraints of selecting a location anywhere within this radius are equally low compared to the benefit of habitat selection. Alternatively, if costs or constraints increase with distance, then, independent of habitat, we should observe higher frequencies of short moves than long moves. In this situation, a negative-exponential distribution may be a better descriptor of habitat-independent movement distances. Therefore, the two alternative habitat independent-movement probability functions differed in the assumptions that they make about the importance of movement costs or constraints.

For the availability radius model, the habitat-independent movement probability function in two dimensions is

$$\phi(a, b) = \begin{cases} \dfrac{1}{\pi R^2} & \text{if } r_{ab} \leq R \\ 0 & \text{if } r_{ab} > R \end{cases} \tag{4}$$

where R is the radius of available area and r_{ab} is the distance between locations a and b (see Appendix B). For the negative-exponential model, the habitat-independent movement probability function in two dimensions is

$$\phi(a, b) = \frac{\lambda \, \exp(-\lambda r_{ab})}{2\pi r_{ab}} \tag{5}$$

where λ is the scale parameter for the negative-exponential distribution (see Appendix B).

In Eqs. 1–3, the habitat preference parameters, w_j, are assumed to be constant. However, they can be specified to depend upon covariates, X_i, such that

$$w_j(X_i) = \exp(\alpha_j + \beta' X_i) \tag{6}$$

where α_j is an intercept parameter for habitat j; X_i is a vector of spatial and/or nonspatial covariates relating to move i; β is a vector of coefficients on X_i and $w_j(X_i)$ is the habitat selection parameter for habitat type j, given the covariates, X_i. The α_j parameters determine the value of the w_js when all covariates are equal to zero and the parameters in β determine how this changes with the covariates. In practice, α_j for one habitat was set to zero and the intercepts for the other habitat types were estimated relative to this. Similarly, covariates could be specified for λ, but we restrict the discussion in this paper to covariates in the w_js.

We modeled home range behavior by incorporating the distance to the home range center as a spatial covariate in the w_js, with coefficient β_{hr}. For each individual, we calculated the location of the home range center for each move, i, as the bivariate mean of all the recorded locations for the individual, excluding the

location moved to in move i. This approach introduces spatial dependence between all locations because each move is a function of all other observed locations, in addition to the individual's current location and the distribution of habitat. The term in the model for the distance to the home range center performs the same function as the autocorrelation term in spatial autoregressive models (e.g., Augustin et al. 1996). A similar dependency on the home range center was assumed by Moorcroft et al. (1999) for modeling coyote home ranges, except that they used the centroid of observations. We used the bivariate mean, but if data are thought to contain outliers, then measures of the center of activity that are more robust to outliers, such as trimmed means, may be considered instead (Koeppl et al. 1985).

The value of the coefficient β_{hr} is interpreted as the change in $\ln(w_j)$ for a unit change in distance from the home range center. Our assumption was that there is some central tendency of movements toward a center of activity, independent of habitat. For animals with this tendency, we would expect β_{hr} to be negative, implying a lower probability of selecting a habitat far from the home range center than a habitat close to the home range center. This introduces movement bias back toward the home range (e.g., Holgate 1971), and is a departure from previous models in that it formulates the habitat selection parameters as a function of their spatial location.

Parameter estimation

Maximum likelihood parameter estimates were obtained by substituting Eqs. 4 or 5 and Eq. 6 into Eq. 3 and maximizing this function for the unknown parameters, λ, β_{hr}, and α_j. This was achieved by minimizing the negative log-likelihood, $L = -\ln(\ell)$, using Powell's method for multidimensional minimization (Press et al. 1992, Hilborn and Mangel 1997). The variance–covariance matrix of the parameters was estimated as the inverse of the matrix of negative log-likelihood second derivatives calculated at the maximum likelihood parameter values (Fisher 1922, Arthur et al. 1996). The Akaike's information criterion (AIC) was calculated for each model as $2L + 2p$, where p is the number of parameters. Model fitting was achieved using a C++ program written with Borland C++ Builder 5.0 (Borland 2000).

Application to a koala radio-tracking data set

Koalas are large, folivorous, arboreal marsupials restricted to the eucalypt forests of eastern and southeastern Australia. They feed on a wide range of tree species, predominantly from the genera *Eucalyptus* and *Corymbia*, but tend to show preferences for only a few species in any one location (Hindell and Lee 1990). Koalas occupy reasonably well-defined home ranges and, although they are largely solitary, both male and female home ranges can overlap (Mitchell 1990, White 1999, Ellis et al. 2002).

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TABLE 1. Model rankings (most parsimonious models at the top), Akaike's information criteria (AIC), and parameter estimates.

Model	AIC	λ	α_{sec}	α_{marg}	α_{sand}	α_{clear}	α_{other}	β_{hr}
Females								
nehrhab	49 880.30	4.77×10^{-3}	0.016	−0.231	−0.471	−0.736	−0.504	-3.71×10^{-3}
nehr	49 936.57	4.91×10^{-3}						-3.82×10^{-3}
nehab	50 470.60	5.90×10^{-3}	0.017	−0.263	−0.439	−0.866	−0.683	
ne	50 566.56	6.11×10^{-3}						
arhrhab	59 712.20		0.106	−0.517	−0.663	−1.231	−0.955	-5.70×10^{-3}
arhr	59 987.26							-5.92×10^{-3}
arhab	66 637.74		0.744	−0.222	−0.783	−1.908	−1.425	
ar	67 728.86							
Males								
nehrhab	40 563.28	2.51×10^{-3}	−0.061	−0.285	−0.337	−0.392	−0.468	-2.52×10^{-3}
nehr	40 576.44	2.54×10^{-3}						-2.52×10^{-3}
nehab	41 114.20	3.39×10^{-3}	0.033	−0.187	−0.063	−0.388	−0.499	
ne	41 135.58	3.44×10^{-3}						
arhrhab	44 189.34		−0.073	−0.387	−0.602	−0.765	−0.664	-4.23×10^{-3}
arhr	44 250.42							-4.24×10^{-3}
arhab	48 237.54		0.345	−0.072	0.355	−0.967	−0.907	
ar	48 500.50							

Notes: Model abbreviations: ne denotes the negative-exponential model; ar denotes the availability radius model; hr denotes that a distance to home range center term, β_{hr}, is included; and hab indicates that intercepts, α_j, for each habitat type are included. Subscripts of the intercepts are defined as follows: sec, secondary habitat; marg, marginal habitat; sand, sand mining revegetation; clear, cleared land; other, other vegetation. The intercept for primary habitat is fixed at zero.

We fitted the previously described models to a koala radio-tracking data set, consisting of pairs of daily observations, from the Port Stephens Local Government Area, New South Wales, Australia. The data consisted of radio-tracking locations for 24 female and 21 male koalas occupying home ranges. We used a modified version of an existing, independently derived, koala habitat map as the underlying landscape (Lunney et al. 1998). This map consisted of an ArcGIS (ESRI 2002) raster grid with a 50 × 50 m cell size, representing the distribution of six habitat categories: (1) primary habitat, (2) secondary habitat, (3) marginal habitat, (4) sand mining revegetation, (5) cleared land, and (6) other vegetation not classified as koala habitat. A detailed description of the study area, habitat mapping, and radio-tracking data can be found in Appendix C.

For the availability radius and the negative-exponential models, all alternative models with and without (i.e., parameter values fixed at zero) habitat selection parameter intercepts, α_j, and with and without a coefficient, β_{hr}, for the distance to the home range center, were fitted separately to the male and female data. The intercept for primary habitat was fixed at zero; thus all intercept parameters were interpreted relative to primary habitat. A positive intercept implied a higher preference than primary habitat, and vice versa for a negative intercept. This resulted in eight alternative models for each sex, which were ranked by their AIC values (Burnham and Anderson 2002).

RESULTS

The ranking of alternative models showed the same pattern for males and females. There was greater support for the negative-exponential than the availability radius model, for models with habitat selection parameters rather than without, and for models with a distance to home range center term rather than without (Table 1; see Appendix D for the standard errors of the parameter estimates). For both sexes, the most parsimonious model was a negative-exponential model with habitat selection and a distance to home range center term. Differences in AICs suggested little relative support for any of the other models (Burnham and Anderson 2002). For a species that occupies relatively well-defined home ranges, the importance of the home range parameter was not surprising. However, once the effect of the home range was controlled for, selection between habitat types was still important.

The fitted models indicated a general preference for primary and secondary habitat over marginal habitat, sand mining revegetation, cleared land, and other vegetation (Table 1). However, for the males, habitat preference rankings did differ somewhat between models. Further, absolute differences between habitat preference intercepts tended to be larger, implying stronger preferences, in the availability radius models than in the negative-exponential models.

On average, the females moved smaller daily distances than the males. For the negative-exponential models, this was evident from the greater probability mass close to zero for females than for males in the predicted distribution of habitat-independent movement distances (Fig. 1A). The females also exhibited a greater bias toward the home range center, implying smaller home ranges than the males (Fig. 1B).

DISCUSSION

Habitat selection in koalas is commonly linked to preferences for particular tree species (Hindell and Lee
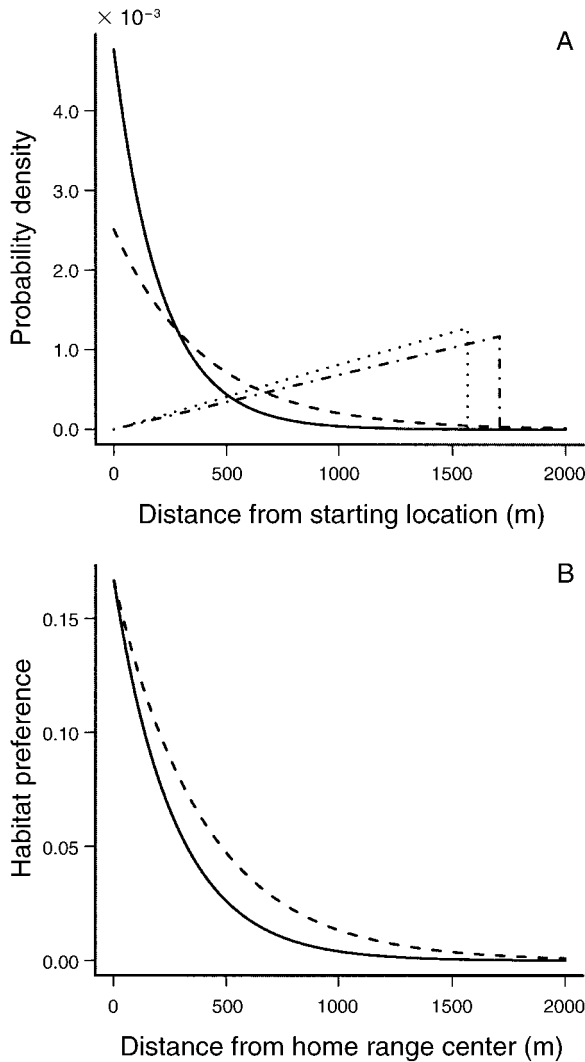
FIG. 1. (A) The fitted probability density functions for the habitat-independent one-day movement distances for: (1) the most parsimonious negative-exponential model (nehrhab, Table 1) for females (solid line) and males (dashed line), and (2) the most parsimonious availability radius model (arhrhab, Table 1) for females (dotted line) and males (dot-dashed line). (B) The fitted decline in habitat preference parameters, w_j, with distance from the home range center for the most parsimonious negative-exponential model (nehrhab, Table 1) for females (solid line) and males (dashed line). For ease of interpretation, this graph shows the behavior of habitat preferences for the case in which all habitat preference parameters are equal and standardized to sum to 1.

1990, White 1999). The underlying habitat categories used in our koala example provided an a priori ranking of habitat quality, based upon the proportion of preferred tree species (particularly *Eucalyptus robusta* and *Eucalyptus parramattensis*) in each vegetation association (Lunney et al. 1998). Previously, koala preferences for particular tree species in Port Stephens had been inferred by the distribution of fecal pellets at the landscape scale (Phillips et al. 2000). Our models now

indicate that, even at a within-home-range scale, koalas are preferentially selecting vegetation associations with high proportions of these tree species (i.e., primary and secondary habitat). However, there was little difference between the preference shown for primary compared to secondary habitat, indicating that these habitat categories may be similar in quality. In common with many other studies, our approach also indicated a tendency for females to have smaller home ranges than males (Mitchell 1990, White 1999, Ellis et al. 2002). Importantly, the methods presented in this paper account for this difference when estimating the underlying habitat preferences.

A common issue for habitat selection models of movement data is violation of the assumption of independence between locations and individuals (Swihart and Slade 1985). This can be particularly problematic for animals occupying well-defined home ranges. One solution is to subsample the data to reduce autocorrelation, but this can lead to a dramatic loss of information and may be misleading if spatial correlation is an intrinsic property of the movement process (Swihart and Slade 1985, De Solla et al. 1999). In the example that we provided, locations were often significantly correlated even after several weeks and so subsampling the data would have been impractical. A superior approach is to explicitly incorporate autocorrelation into the models (Legendre 1993). We achieved this by modeling movement as conditional on the location of each individual's home range. In addition, by defining a habitat-independent movement probability function, relative to an individual's current location, we accounted for dependence between successive locations (sensu Arthur et al. 1996).

We made the assumption that the underlying distribution of distances moved was independent of the habitats moved through. This may be broadly true for animals making discrete choices of habitat from a cognitive map of the area and moving directly to the chosen habitats. On the other hand, if habitat type influences both the speed at which individuals move and the amount of time that they spend foraging, then it may be difficult to define movement distances independent of habitat. This could be particularly problematic for animals that are moving more or less continuously (Hjermann 2000). An extension to the model, to accommodate this, could be to formulate the underlying movement probabilities as a function of habitat. Regardless, choosing the right function may be difficult without some prior information about factors affecting movement patterns. This choice is important because different functions can imply quite different habitat preferences and predicted movement patterns (Fig. 1, Table 1, Appendix B).

In the face of these uncertainties, we took a Lakatosian approach, which involves taking a set of, a priori, hypotheses (model structures) and formally assessing the support for each hypothesis using data (Lakatos

1978, Hilborn and Mangel 1997, Burnham and Anderson 2002). Applying the methods that we have presented in such a way provides an objective means of comparing alternative hypotheses on the importance of habitat selection relative to other spatial processes. In the koala example, the negative-exponential, habitat-independent movement probability function and the distance to home range center term both had a high level of support from the data. This suggests that koala movements are constrained by factors other than pure habitat selection. However, habitat selection was still important because the most parsimonious descriptors of the data also included the habitat preference parameters. Support for a distance to home range term can be explained by home range behavior. Support for a declining habitat-independent movement probability function may be explained by high movement costs relative to the benefits of habitat selection, but this could also be a reflection that movements are constrained within a home range. One explanation may be that, because koalas have a low-quality food source and low metabolic rate (Cork and Sanson 1990), frequent long-distance movements are costly.

We made the assumption that individuals had a single center of activity, toward which movements were biased. Most of the individuals in the koala example broadly met this assumption, but individuals of some species can have multiple centers of activity, such as multiple den sites. One way to account for this would be to include multiple terms for the distances to each of the centers of activity. Dealing with species that have more complex home range behaviors should be an important consideration for future research because this will have ramifications for the broad application of these models.

Another important area of research will be to consider how to deal with the nested structure of most movement data, i.e., radio-tracking locations nested within individuals. We assumed that variation within and between individuals was the same. However, data points within individuals will tend to be more highly correlated than those between individuals. This problem is commonly overcome by taking the individual as the sampling unit (Aebischer et al. 1993), but this would make the incorporation of spatial parameters more difficult. An alternative approach would be to formulate the model as a mixed-effects model (Pinheiro and Bates 2000), but as far as we are aware, this is yet to be done.

Habitat selection is an inherently spatial process and therefore it is important that habitat selection models for analyzing movement data incorporate these processes in an easily interpretable way. In this paper, we have restricted our analysis to the incorporation of home range behavior, but the approach also can easily be extended to incorporate other spatial process, such as the location of competitors or predators. As such, the methods are generally applicable to a range of species and questions, while providing more biologically meaningful and robust models of habitat selection.

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APPENDIX A

A description of the relationship between the spatially explicit habitat selection model and Arthur et al.'s (1996) model is available in ESA's Electronic Data Archive: *Ecological Archives* E086-066-A1.

APPENDIX B

A derivation of the two-dimensional habitat independent movement probability functions is available in ESA's Electronic Data Archive: *Ecological Archives* E086-066-A2.

APPENDIX C

A description of the study area, habitat mapping, and radio-tracking data and a table of the ratio-tracking data is available in ESA's Electronic Data Archive: *Ecological Archives* E086-066-A3.

APPENDIX D

A table showing the standard errors of the parameter estimates is available in ESA's Electronic Data Archive: *Ecological Archives* E086-066-A4.

REPORTS