

TABLE 4.5 Summary of Model Selection Procedure for Pronghorn Antelope Example Examining Factors Affecting Detection Probabilities, with a General Model for Occupancy (i.e., $\psi(Sg + SI + DW + A)$)

| Model | ΔAIC | w | $-2l$ | $NPar$ |
|-----------------------|--------------|-----|---------|--------|
| $p(DW)$ | 0.00 | 24% | 618.54 | 9 |
| $p(SI + A)$ | 1.37 | 12% | 617.913 | 10 |
| $p(A)$ | 1.75 | 10% | 616.286 | 11 |
| $p(Sg + DW)$ | 1.79 | 10% | 618.325 | 10 |
| $p(DW + A)$ | 1.82 | 10% | 614.36 | 12 |
| $p(\cdot)$ | 2.80 | 6% | 623.345 | 8 |
| $p(Sg + SI + DW)$ | 3.17 | 5% | 617.707 | 11 |
| $p(SI + DW + A)$ | 3.56 | 4% | 614.1 | 13 |
| $p(Sg + DW + A)$ | 3.58 | 4% | 614.116 | 13 |
| $p(Sg + A)$ | 3.62 | 4% | 616.157 | 12 |
| $p(SI + A)$ | 3.73 | 4% | 616.274 | 12 |
| $p(SI)$ | 4.76 | 2% | 623.305 | 9 |
| $p(Sg)$ | 4.79 | 2% | 623.332 | 9 |
| $p(Sg + SI + DW + A)$ | 5.15 | 2% | 613.691 | 14 |
| $p(Sg + SI + A)$ | 5.61 | 1% | 616.153 | 13 |
| $p(Sg + SI)$ | 6.75 | 1% | 623.295 | 10 |

Given are the relative difference in AIC values compared to the top-ranked model (ΔAIC); the AIC model weights (w); twice the negative log-likelihood ($-2l$); and the number of parameters in the model ($NPar$).

also affecting detection probabilities. Subsequent modeling supports this premise. The results of performing model selection on the detection probabilities while maintaining a general model for occupancy (i.e., $\psi(Sg + SI + DW + A)$) are presented in Table 4.5. The summed model weights for the factors with respect to detection probability are: distance to water source: 68%; aspect: 37%; slope: 29%; and sagebrush density: 27%. Clearly, there is moderately strong support that detection probability is affected by distance to water and less support for the other factors. Interestingly, note that the model with constant detection probability ($p(\cdot)$, the de facto assumption when using simple logistic regression) has only a very low model weight, suggesting little support for this hypothesis.

Mahoenui Giant Weta

Weta are ancient species of the order *Orthoptera* (e.g., grasshoppers, crickets, and locusts), with more than 70 endemic species surviving in New Zealand today. Based upon fossil records, they have remained almost unchanged from their ancestors of 190 million years ago. In the absence of native ground-

| -2l | NPar |
|--------|------|
| 8.54 | 9 |
| 7.913 | 10 |
| 6.286 | 11 |
| 8.325 | 10 |
| 4.36 | 12 |
| 23.345 | 8 |
| 17.707 | 11 |
| 4.1 | 13 |
| 4.116 | 13 |
| 16.157 | 12 |
| 16.274 | 12 |
| 23.305 | 9 |
| 23.332 | 9 |
| 13.691 | 14 |
| 16.153 | 13 |
| 23.295 | 10 |

ranked model (ΔAIC); the number of parameters in

Modeling supports this detection probability, $\psi(Sg + Sl + DW + \dots)$ for the factors with effect: 68%; aspect: 37%; is moderately strong effect to water and less model with constant in using simple logis- tics little support for

grasshoppers, crickets, living in New Zealand most unchanged from effect of native ground-

dwelling mammals, the weta of New Zealand evolved to fulfill the roles rodents play in other ecosystems. As such, the introduction of rats and other small mammals to New Zealand ecosystems with the arrival of the Maori and Europeans decimated weta populations.

The Mahoenui giant weta (*Deinacrida mahoenui*) is endemic to the King Country on the North Island of New Zealand, with only two surviving populations. The main naturally occurring population is restricted to a 240-ha scientific reserve at Mahoenui (near the town of Te Kuiti) maintained by the New Zealand Department of Conservation. The reserve is characterized by steep-sided gullies and is largely covered by dense gorse (*Ulex europaeus*), a perennial pest plant with sharp spiny stems and bright yellow flowers that can form dense thickets, originally introduced to New Zealand as a hedging plant by the early European settlers. The weta use the prickly gorse plants as protection from predators and also as a food source. Goats and cattle are used to browse the gorse, encouraging dense foliage and providing further protection for weta.

As part of a pilot study, in March 2004, 72 circular plots of 3 m radius were surveyed for the Mahoenui giant weta within the more accessible regions of the reserve. Clearly, inference can only be made as to the more accessible parts of the reserve, but this was deemed reasonable given the nature of the pilot study. Each plot was surveyed between three and five times during the five-day period ($K_{average} = 3.6$). Three different observers were used, and the study was designed such that each observer surveyed each site at least once. This was done to avoid introducing heterogeneity in detection probabilities caused by the use of multiple observers (see Chapter 6 for further discussion).

Weta were detected at 35 of the 72 plots (a naïve occupancy estimate of 0.49); however, often weta were only detected in one or two of the repeated surveys, clearly indicating that detection probabilities are less than 1. There conceivably may be a number of plots where weta were indeed present but simply never detected during the surveys.

Here we wish to estimate the probability of occupancy for the weta. Detection probabilities will be allowed to vary by day and also among observers, but simpler models that do not include these effects will be included in our candidate set also in the interests of parsimony. Daily variation in detection probabilities (or more generally, survey-specific detection probabilities) can be easily accommodated with the design-matrix interface used in PRESENCE 2.0 to build models. To allow detection probabilities to vary among the three observers, two survey occasion-specific covariates were defined, *Obs1* and *Obs2*. For site *i*, survey *j*, *Obs1* = 1 if the survey was conducted by observer 1, 0 otherwise; and *Obs2* = 1 if the survey was conducted by observer 2, 0 otherwise. Note that if the survey was conducted by observer 3, then *Obs1* = 0 and *Obs2* = 0; thus, the third observer is considered the standard or reference observer against which the other observers are to be compared (Table 4.6).

TABLE 4.6 Coding Used to Define Observer Effects in Mahoenui Giant Weta Example Using the *Obs1* and *Obs2* Covariates

| Survey conducted by | <i>Obs1</i> | <i>Obs2</i> |
|---------------------|-------------|-------------|
| Observer 1 | 1 | 0 |
| Observer 2 | 0 | 1 |
| Observer 3 | 0 | 0 |

TABLE 4.7 Summary of Model Selection Procedure for Mahoenui Giant Weta Example

| Model | ΔAIC | w | $NPar$ | $-2l$ | <i>Browse</i> | SE |
|-------------------------------------|--------------|------|--------|--------|---------------|------|
| $\psi(Browse)p(Day + Obs)$ | 0.00 | 0.27 | 9 | 239.60 | 1.17 | 0.74 |
| $\psi(\cdot)p(Day + Obs)$ | 0.95 | 0.17 | 8 | 242.55 | | |
| $\psi(\cdot)p(Day + Obs + Browse)$ | 1.81 | 0.11 | 9 | 241.41 | | |
| $\psi(Browse)p(Day)$ | 1.84 | 0.11 | 7 | 245.44 | 1.24 | 0.75 |
| $\psi(Browse)p(Day + Obs + Browse)$ | 2.00 | 0.10 | 10 | 239.60 | 1.17 | 0.89 |
| $\psi(\cdot)p(Day)$ | 3.19 | 0.06 | 6 | 248.79 | | |
| $\psi(\cdot)p(Day + Browse)$ | 3.58 | 0.05 | 7 | 247.18 | | |
| $\psi(Browse)p(Day + Browse)$ | 3.81 | 0.04 | 8 | 245.41 | 1.15 | 0.88 |
| $\psi(Browse)p(Obs)$ | 4.44 | 0.03 | 5 | 252.04 | 1.18 | 0.70 |
| $\psi(\cdot)p(Obs)$ | 5.76 | 0.02 | 4 | 255.36 | | |
| $\psi(\cdot)p(Obs + Browse)$ | 6.20 | 0.01 | 4 | 255.80 | | |
| $\psi(Browse)p(Obs + Browse)$ | 6.42 | 0.01 | 6 | 252.02 | 1.25 | 0.83 |
| $\psi(Browse)p(\cdot)$ | 6.66 | 0.01 | 3 | 258.26 | 1.23 | 0.72 |
| $\psi(\cdot)p(\cdot)$ | 8.19 | 0.00 | 2 | 261.79 | | |
| $\psi(Browse)p(Browse)$ | 8.66 | 0.00 | 4 | 258.26 | 1.20 | 0.84 |
| $\psi(\cdot)p(Browse)$ | 8.85 | 0.00 | 3 | 260.45 | | |

ΔAIC is the difference in AIC value for a particular model when compared with the top-ranked model; w is the AIC model weight; $NPar$ is the number of parameters; $-2l$ is twice the negative log-likelihood value; *Browse* is the value of the coefficient for the *Browse* variable with respect to its effect on occupancy probability; and SE is the associated standard error (blank entries indicate that the *Browse* variable was not included in the models).

The estimated coefficients related to the covariates *Obs1* and *Obs2* therefore represent the difference (on the logistic scale) between the respective observers and observer 3. While the pilot study was not specifically designed for this purpose, the effect of browsing on occupancy and detection probability will also be assessed. The level of browsing at each plot was assessed by the field crew prior to the pilot study, and a covariate *Browse* has been defined here as = 1 if the plot showed evidence of sustained browsing (based upon shape of bushes and foliage density), 0 otherwise. Therefore, our candidate set contains 16 models without considering interactions between factors (Table 4.7).

in
Obs2

Obs2

0
1
0

Weta Example

| Browse | SE |
|--------|------|
| 1.17 | 0.74 |
| 1.24 | 0.75 |
| 1.17 | 0.89 |
| 1.15 | 0.88 |
| 1.18 | 0.70 |
| 1.25 | 0.83 |
| 1.23 | 0.72 |
| 1.20 | 0.84 |

with the top-ranked
is twice the negative
variable with respect to
blank entries indicate

and Obs2 therefore
pective observers
designed for this
a probability will
essed by the field
n defined here as
ed upon shape of
andidate set contains
ctors (Table 4.7).

Models are denoted with the relevant factors indicated in parentheses following each probability. For example, $\psi(\text{Browse})$ indicates the probability of occupancy being different for browsed and unbrowsed sites, while $p(\text{Day} + \text{Obs})$ indicates that detection probability varied by day with additive (on the logistic scale) observer effects.

Testing the global model from the candidate set, $\psi(\text{Browse})p(\text{Day} + \text{Obs} + \text{Browse})$, does not indicate any evidence of lack of fit using 10,000 bootstrap samples ($X^2 = 154.1$, $P\text{-value} = 0.999$, $\hat{c} = 0.35$), although one would perhaps be concerned that the P -value is so close to 1.0 that it may indicate the model "over-fits" the data (i.e., there may be too many parameters in the model). As such, no adjustment has been made to the model selection procedure (AIC) or the standard errors of parameter estimates.

Table 4.7 presents the 16 models ranked according to AIC. The first thing to note is that no single model is demonstrably better than the others; the five top models are separated by less than 2.0 AIC units. As such, the AIC model weight is distributed across a number of models, indicating that a number of models may be reasonable for the collected data. There are, however, a number of common features among the top-ranked models. The eight models where detection probability varied daily are all ranked higher than the models without daily variation. In terms of model weights, the $p(\text{Day})$ models have 91% of the total, providing clear evidence that *Day* is an important factor in terms of accurately modeling detection probabilities. In terms of comparing hypotheses, the hypothesis that the detection probability varied among days therefore has much greater support than the hypothesis that it was constant. Many of the top-ranked models also contain the factor *Obs* for detection probability, providing evidence that the observers differed in their ability to find weta in the plots. The combined model weight for $p(\text{Obs})$ models is 73%. There is substantially less support for the hypothesis that the level of browse affects detection probabilities, with a combined model weight of 33%.

In terms of occupancy probability, based upon rankings and AIC model weights, the results are somewhat inconclusive about the effect of browse. The combined weight for the $\psi(\text{Browse})$ models is 58%—in other words, similar levels of support for the hypotheses that occupancy is/is not affected by whether bushes within the plots are browsed. However, there is an important point to note that illustrates that unthinking use of model selection procedures can be misleading. Given the biology of the situation, *a priori* we would expect browsing to increase the probability of occupancy (by creating better habitat); therefore the parameter estimate associated with the factor *Browse* for occupancy should be positive. This was in fact the case (Table 4.7). From the respective models, all estimates for the *Browse* factor were very similar. Yet AIC and similar metrics (and therefore the derived model weights) do not account for the fact that one could specify *a priori* the direction of a particular rela-

tionship (i.e., one could very loosely describe these model selection procedures as "two-sided"). Therefore, one could argue that, as the estimated effect matches our *a priori* expectations, the level of support for these models should be greater than that indicated by the model weights. Unfortunately, we cannot make any firm recommendations at this time for how one might objectively incorporate this idea into an information-theoretic framework. As such, when interpreting the magnitude of the various effects below, rather than taking a model-averaging approach to account for uncertainty about which model(s) provides the most efficient representation of the data, we only consider the parameter estimates from the top-ranked model. We acknowledge that our standard errors do not account for model selection uncertainty (Burnham and Anderson 2002).

From the model $\psi(\text{Browse})p(\text{Day} + \text{Obs})$ we have the following equations for estimating occupancy and detection probabilities:

$$\text{logit}(\psi_i) = 0.02 + 1.17\text{Browse}_i \quad (4.11)$$

and:

$$\begin{aligned} \text{logit}(p_{ij}) = & -0.23\text{Day}1 - 0.38\text{Day}2 - 1.17\text{Day}3 - 0.30\text{Day}4 \\ & + 0.81\text{Day}5 - 1.07\text{Obs}1_{ij} - 0.34\text{Obs}2_{ij} \end{aligned} \quad (4.12)$$

where Browse_i is the value of the variable *Browse* for plot *i* (1 or 0); *Day*1–*Day*5 are just indicator variables for the day of the study; and $\text{Obs}1_{ij}$ and $\text{Obs}2_{ij}$ are used to denote which of the three observers surveyed a given site on a given day (see Table 4.6).

From Eq. (4.11), for an unbrowsed site $\text{logit}(\psi_i) = 0.02$ (as $\text{Browse}_i = 0$), which gives odds of occupancy of $e^{0.02} = 1.02$ (:1) and a probability of occupancy of $1.02/(1 + 1.02) = 0.50$. To interpret the effect of browsing on the probability of occupancy, we shall do so in terms of odds ratios (see Chapter 3). The odds ratio for a browsed site being occupied by weta is $e^{1.17} = 3.22$; hence, the odds of occupancy at a browsed site is $3.22 \times 1.02 = 3.28$ (:1; or a probability of occupancy of $3.28/(1 + 3.28) = 0.77$). A confidence interval for the effect of browsing could be calculated on the logit scale, then transformed to the scale of an odds ratio. For example, given that the standard error for the estimated *Browse* effect is 0.74, an approximate two-sided 95% confidence interval on the logit scale would be $1.17 \pm 2 \times 0.74 = (-0.31, 2.65)$, giving an interval of $(e^{-0.31}, e^{2.65}) = (0.73, 14.15)$ for the odds ratio. As mentioned in Section 3.4, an odds ratio of 1.0 would indicate that the factor has no effect; hence, as 1.0 is included in the confidence interval, we do not have strong evidence that browsing has an effect on the probability of occupancy by weta. Although, as it was expected *a priori* that browsing should have a positive effect on occupancy, it would be more appropriate to consider a one-sided 95%

confidence interval (or a one-sided 90% confidence interval on the logit scale, or (0.95, $e^{2.65}$) confidence interval, where $e^{2.65} = 14.15$). Here, browsing has a positive effect on occupancy, but the effect is only poorly known.

In terms of an overall estimate, we can calculate an average probability of occupancy for browsed and unbrowsed sites. Here, 35 plots were browsed and 35 plots were unbrowsed. The overall estimate would be

$$\frac{S_{\text{Browsed}} \hat{\Psi}_{\text{Browsed}} + S_{\text{Unbrowsed}} \hat{\Psi}_{\text{Unbrowsed}}}{S_{\text{Browsed}} + S_{\text{Unbrowsed}}}$$

This is 30% larger than the estimate for unbrowsed sites (species was detected) and 30% smaller than the estimate for browsed sites. If we increased the estimate for browsed sites, the overall estimate would increase. This is applicable in this example as a conservative method for obtaining an overall estimate. The best estimate would be to predict the probability of occupancy for each plot. For example, suppose the probability of occupancy for each plot was surveyed. The overall estimate would be the average of the model(s). If the variance of the estimate is available for all grid cells, the overall estimate of occupancy probability for each plot would simply be the average of the probability within the region of interest.

The variance (or standard error) of the overall estimate is calculated in two steps. First, the variance for an unbrowsed plot using the logit scale is calculated. The variance terms in the normal distribution are

$$\text{Var}(\hat{\Psi}_{\text{Overall}}) = \frac{1}{n} \left(\frac{1}{S_{\text{Browsed}}} + \frac{1}{S_{\text{Unbrowsed}}} \right) s^2$$

where the s^2 terms represent the variance of the logit scale. It is important to note that the variance of the logit scale is not the same as the variance of the probability scale.

confidence interval (calculated here by taking the lower limit of a two-sided 90% confidence interval). That is, $(1.17 - 1.65 \times 0.74, \infty) = (-0.05, \infty)$ on the logit scale, or $(0.95, \infty)$ in terms of odds ratios. As 1.0 is only just inside the confidence interval, we would be comfortable in concluding that it does appear browsing has a positive effect on occupancy, but the magnitude of the effect is only poorly known.

In terms of an overall estimate of occupancy, for the plots surveyed we could calculate an average from the estimated occupancy probabilities for the browsed and unbrowsed plots, weighted by the number of plots of each type. Here, 35 plots were classified as browsed and 37 classified as unbrowsed. An overall estimate would therefore be:

$$\begin{aligned} \frac{s_{Browsed} \hat{\Psi}_{Browsed} + s_{Unbrowsed} \hat{\Psi}_{Unbrowsed}}{s_{Browsed} + s_{Unbrowsed}} &= \frac{35 \times 0.77 + 37 \times 0.50}{35 + 37} \\ &= \frac{26.95 + 18.5}{72} \\ &= \frac{45.45}{72} \\ &= 0.63 \end{aligned}$$

This is 30% larger than the naïve estimate (the fraction of plots where the species was detected) of 0.49. Clearly, accounting for detection probability has increased the estimated level of occupancy as expected (see below). While not applicable in this example due to the nature of the study design, an alternative method for obtaining an overall estimate of occupancy for the area of interest would be to predict occupancy at each of the potential sampling units. For example, suppose the area could be divided into grid cells (say) of which a sample was surveyed and the resulting data used to build an occupancy model(s). If the variable information used within the occupancy model was available for all grid cells within the regions (e.g., from GIS), then the occupancy probability for each cell could be predicted, and the total level of occupancy would simply be the sum of the occupancy probabilities for all grid cells within the region of interest.

The variance (or standard error) for the overall level of occupancy can be calculated in two steps. First, calculate the variance for a browsed and unbrowsed plot using the delta method (Chapter 3), then combine these variance terms in the normal manner for a weighted average; that is:

$$\text{Var}(\hat{\Psi}_{Overall}) = \frac{s_{Browsed}^2 \text{Var}(\hat{\Psi}_{Browsed}) + s_{Unbrowsed}^2 \text{Var}(\hat{\Psi}_{Unbrowsed})}{(s_{Browsed} + s_{Unbrowsed})^2},$$

where the s^2 terms relate the number of plots squared, not a sample variance. It is important to note that the full variance-covariance matrix is for all the β

