

## **CHAPTER 4**

### **FORAGING ECOLOGY AND BEHAVIOR**

#### **ABSTRACT**

The endangered South Australian glossy black-cockatoo feeds almost exclusively on the seeds of the drooping sheoak tree, and shows marked preferences among trees. This field study used observations of foraging birds and measurements of trees and seed cones to investigate foraging ecology and tree selection. The vast majority of foraging time (94%) was spent handling cones, and cone handling behaviour was highly stereotyped. Handling time per cone was determined primarily by cone size, while seed intake rate was determined primarily by seed mass per cone. The cockatoos usually foraged in trees that showed signs of previous foraging. New trees that they choose to sample had relatively large seeds, and of the sampled trees they accepted those with high ratios of seed to cone mass. The trees they fed in differed from nearby unused trees in being larger, and having more total seed per cone, higher ratios of seed to cone mass, and larger seeds with more lipid and protein. Combining seed intake rate and nutritional quality, tree selection increased the rate of energy intake by an estimated 28%. Although insect larvae were present in some seed cones, the cockatoos did not actively seek them. Males foraged 20% more efficiently than females, resulting in greater daily food intake.

## INTRODUCTION

Glossy black-cockatoos *Calyptorhynchus lathami* are unique among Australian parrots in their degree of foraging specialization. All authors agree that they feed almost exclusively on *Allocasuarina* seed cones throughout their range (e.g., Cleland and Sims 1968, Reader's Digest 1976, Joseph 1982, Blakers *et al.* 1984, Baxter 1989, Clout 1989, Forshaw 1989). This makes their foraging ecology easier to study than that of most species, because their feeding rates and nutritional intake can be accurately quantified. Their feeding specialization also makes them more vulnerable from a conservation perspective, which is a particular concern for the small and isolated South Australian subspecies, *C. l. halmaturinus* (Chapter 2).

An earlier study of the foraging ecology of *C. l. lathami* in New South Wales found that they foraged exclusively on *A. littoralis*, and showed marked preferences for individual trees, preferring those with high ratios of seed to cone weight (Clout 1989). On Kangaroo Island, South Australia, *C. l. halmaturinus* feeds almost exclusively on drooping sheoak, *Allocasuarina verticillata*, and also shows strong preferences among trees (Chapter 2). The current study investigated the foraging ecology of the South Australian glossy black-cockatoo, focusing on tree selection, foraging profitability, and their importance to habitat selection and conservation biology.

Drooping sheoaks are dioecious, and female trees bear woody cylindrical or barrel-shaped seed cones 20 - 50 mm long and 17 - 30 mm in diameter, on a short (0 - 10 mm) stem (Wilson & Johnson 1989). Seed cones are composed of radially arranged valves which open after maturity to release a small dry one-winged fruit (samara) containing one seed. Although technically a samara consists of a seed and its surrounding fruit, I will refer to them here as seeds. Drooping sheoaks prefer shaley soil, and on

Kangaroo Island they occur mainly along the north coast and on steep slopes in inland waterways. Although they also occur mixed with eucalypts, in the study area they were present primarily as pure stands. Seed cones are retained on the tree after maturity, and do not usually release their seeds for more than a year, so that seed-bearing cones are present year round. Newly mature cones are a reddish brown, and as they age they become darker brown and then gray over several years. New cones are produced mainly near the ends of branches, and different cohorts of cones can be distinguished by their color.

## **METHODS**

Foraging data were collected between April 7 and May 24 1993 (during the nesting season) in an area of approximately four hectares in Latham Conservation Park on the north coast of Kangaroo Island, South Australia. The area included a mosaic of stands of varying ages and fire histories, as evidenced by the presence of multi-stemmed trees typical of basal re-shooting following a fire. A total of seventeen individually identified cockatoos were observed, including eight paired females, seven paired males, and two unpaired males. All had adult plumage except one paired female with no yellow markings on the head, which is characteristic of subadults. Individual females were identified by distinctive plumage markings on the head and tail, and males were identified either by plumage markings (four males), missing flight feathers (two males), or only by consistent close association with a known female (three males). Data were also collected on several unpaired males that were not identified individually. Only one pair had an active nest during the study.

## **Observation of Foraging Birds**

In order to sample as evenly as possible from different individuals a priority list was used to search for those that had been observed less frequently. To begin a sampling session we walked through the study area until we encountered an individual from the priority list. The session included observations on the initial subject, its mate if paired, any birds that shared a foraging tree with the initial subjects, and their mates. An individual feeding in one tree was considered a bout, so an observation session included at least one bout for each foraging cockatoo present, or more if they changed trees during the session. We recorded the times at which the subject first touched each cone and dropped it, whether the cone was partially or completely shredded, and whether the cockatoo paused for more than five seconds while handling the cone. For each bout we recorded at least 10 complete cone handling times when possible. We also noted the individual and tree involved, number of cones eaten, and whether the subject left the tree to forage in a different tree.

A session ended either when all the foraging birds left the visible area, or when at least 10 complete handling times had been recorded from each current bout and the cockatoos had been allowed to forage for at least one hour. At the end of the session we counted the total number of chewed cone ends beneath the tree, the number that were only partly eaten, those showing evidence of infestation by parasitic insect larvae, and those chewed from the distal end (leaving the attached stem intact).

During 61 observation sessions we watched the cockatoos eat 1382 cones in 129 bouts in 74 trees. I defined foraging time as excluding inactive periods of more than two minutes and gaps in feeding of more than five minutes, as these were judged not to be part of foraging activity. Foraging was divided into handling times, while the cockatoos were in contact with a seed cone, and intervening search times. For analyses of handling

times I included only cones that were chewed completely without pauses of longer than five seconds, and only bouts with at least 10 handling times.

### **Measurement of Trees and Cones**

At the end of each feeding session we assigned a unique number to each tree the cockatoos had fed in, as well as the drooping sheoak nearest to each that had not been fed in, and that held at least 20 cones. We marked each numbered tree with plastic tape, recorded its girth at 50 cm high, estimated its standing crop of unopened (seed bearing) cones, and recorded whether it had been fed in previously (as evidenced by old chewings on the ground). If there was more than one stem at 50 cm height, we measured each and calculated a single equivalent girth with the same total cross-sectional area, assuming that stems were cylindrical (total girth = square root of the sum of squares of separate girths). To estimate the standing crop of cones we counted the number of cones on 3-4 typical branches and multiplied the number of branches by the number of cones per branch.

From each tagged tree that had not been sampled previously, we collected 20 unopened cones. We attempted to collect this sample from several different branches, picking the first cones our hands fell on without watching (to avoid sampling bias), and sampling from the same age cohort of cones that the cockatoos had foraged on. We dried the cones in a drying oven at 40 C for four days, after which all cones had opened. We shook the cones briskly to separate the seeds, and pulled out any remaining seeds with forceps. We pooled the seeds from each tree and the cones from each tree, and weighed them separately on an electronic balance to the nearest milligram. We calculated mean seed mass per cone for each tree by dividing the total seed mass in the sample by the number of cones. To measure mean seed size, we mixed the seeds thoroughly and counted a sample of 50 to weigh. The number of seeds per cone was calculated for each tree as the seed mass per cone divided by the mean seed size. The relative cone density of

each tree was calculated by regressing cone crop against tree girth, and taking the residuals. For statistical analyses tree girths and cone crops were log transformed to improve normality. Statistical tests were two-tailed unless otherwise noted, and were performed using the SYSTAT software package (Wilkinson 1992).

### **Categorization of Trees**

All trees tagged during the study were assigned to one of four categories for analysis: “Not foraged”, “Preferred”, “Accepted”, or “Rejected”. Trees were categorized as “Not foraged” if they were included as the tree nearest to a foraged tree. (We never saw a cockatoo feed in any of these trees in other sessions.) Trees were categorized as “Rejected” if at least one cone was eaten from the tree, but in each bout observed the subject left to forage in a different tree after eating fewer than 10 cones (excluding cases in which the subject left the tree to join its mate). Trees were categorized as “Preferred” if more than 10 cones were eaten in a bout, the tree was foraged in during more than one session or had chewings under it showing that it had been foraged in previously, and the subject(s) did not leave to forage in another tree. Trees were categorized as “Accepted” if they were foraged in but were neither “Preferred” nor “Rejected”. The final sample included 63 “Not foraged”, 24 “Preferred”, 38 “Accepted”, and 11 “Rejected” trees.

### **Nutritional Analysis**

The pooled seeds from each preference category of foraged trees (“Preferred”, “Accepted”, and “Rejected”), were mixed well and a sample removed for nutritional analysis. I also analyzed seed samples from the first 10 drooping sheoak trees on a transect through the study area. From each tree I collected 20 first-year and 20 second-year cones, and pooled each age class for nutritional analysis. I also included a seed sample pooled from 20 cones from each of 10 arbitrarily chosen large *Allocasuarina*

*muelleriana* trees in a nearby stand where glossy black-cockatoos fed on *A. muelleriana* in the previous year (Pepper 1993). These samples were analyzed by the State Chemistry Laboratories of South Australia for their content of water, protein (= N x 6.25), lipid, ash, crude fiber, and available carbohydrate (= 100% - (water + lipid + protein + ash + crude fiber)). Available energy was calculated from protein (17 kJ/g), lipid (37 kJ/g), and available carbohydrate (17 kJ/g).

## RESULTS

### Description of Female Casuarinas

The measured tree characteristics are summarized in Table 4.1. Multi-stemmed trees comprised 15% of the total, and covered a more restricted size range than single-stemmed trees (23 - 71 cm versus 8 - 114 cm). These trees did not differ from single-stemmed trees in any measured trait except girth (43.4 vs. 34.0 cm, t test with separate variances,  $t = 3.94$ , d.f. = 34.8,  $p < 0.001$ ). Trees with greater girth had more seed cones ( $R = 0.70$ ,  $N = 105$ ,  $p < 0.001$ ). They also had larger cones ( $R = 0.19$ ,  $N = 125$ ,  $p = 0.037$ ), larger seeds ( $R = 0.19$ ,  $p = 0.035$ ) and more total seed mass per cone ( $R = 0.24$ ,  $p = 0.006$ ). The total mass of seed per tree also increased linearly with girth; the regression model was:  $\ln(\text{grams of seed}) = -1.44 + 1.54 * \ln(\text{girth in cm})$  ( $R = 0.69$ ,  $N = 102$ ,  $p < 0.001$ ). Other variables, including empty cone mass and number of seeds, were not correlated with girth. Seed size accounted for 71% of the variance in total seed mass per cone, while the number of seeds explained only 14% (seed size and number of seeds were not significantly correlated). There appeared to be much more variation between than within trees in the shape and size of cones and the size of seeds, but this was not quantified.

We did not observe any vertebrate competitors for drooping sheoak seeds. Crimson rosellas (*Platycercus elegans*) occasionally chewed into closed seed cones, but they did not eat most of the cone, and they appeared to be extracting insect larvae rather than seeds. Finches (*Aegintha temporalis* and *Emblema bellum*) ate seeds from cones as they opened, but did not feed on closed cones.

Table 4.1. Measurements of female drooping sheoak trees, including foraged and unforaged trees. N = number of trees.

	<u>Mean</u>	<u>SD</u>	<u>Min</u>	<u>Max</u>	<u>N</u>
Tree characteristics					
Girth (cm)	35.3	21.5	8.0	114.5	133
Standing crop of seed-bearing cones	262.5	306.8	15	2000	105
Number of stems at 50 cm high	1.2	0.74	1	8	133
Cone characteristics					
Cone size (g)	5.80	1.42	3.00	11.77	125
Empty cone mass (g)	5.46	1.34	2.81	11.23	125
Seed mass per cone (mg)	341	96	169	653	129
Number of seeds per cone	95.9	15.0	67.5	148.6	128
Mean seed size (mg)	3.57	0.95	1.66	6.32	131
Seed as percentage of total cone mass	6.29	1.10	3.13	9.40	129

## **Description of Foraging Behaviour**

The cockatoos fed only on closed drooping sheoak seed cones. Foraging birds were fairly sedentary: observation sessions were usually ended by the observer rather than by the cockatoos leaving the area, and individuals usually fed on only one tree during a session (85% of cockatoo-sessions). Mated pairs usually fed in the same tree, while other individuals often fed nearby but rarely in the same tree. The cockatoos fed only on unopened cones, and usually picked all the cones within reach (an average of 6.25 cones) before walking or climbing a short distance within the tree. Cone handling behavior was very consistent and stereotyped. See Chapter 3 for descriptions of behaviors, and Chapter 7 for a discussion of laterality in feeding behavior. All but three (99.8%) of the 1868 dropped cone ends we examined were distal ends, indicating the cone had been chewed starting at the proximal end. The actual handling of cones occupied 94% of the cockatoos' foraging time. Most cone ends that the cockatoos dropped were quite small and appeared not to contain any seeds, but 15.2% were larger and still contained seeds. Deformation and internal discoloration caused by insect larvae was evident in 7.7% of the cone ends. Cone ends that were dropped before all seeds were extracted often showed evidence of insect infestation, but we did not quantify how often. The empty shells of samaras that had been split open were present in the shredded cone material below trees, but whole seeds were not in evidence. Data on foraging rates are summarized in Table 4.2.

## **Tree Characteristics Affecting Foraging Rates**

To determine which tree characteristics affected search and handling times, I calculated average times for each bout, then averaged the bouts in each tree. Linear regressions showed that search time was correlated only with the tree's relative cone density ( $R = 0.35$ ,  $N = 54$  trees,  $p = 0.01$ ). Handling time per cone was correlated with

Table 4.2. Foraging rates, based on the average value per bout. N = number of bouts.

	<u>Mean</u>	<u>SD</u>	<u>Min</u>	<u>Max</u>	<u>N</u>
Search time per cone (sec)	12.7	8.4	2.7	40.8	87
Handling time per cone (sec)	194.9	40.2	130.2	332.5	90
Feeding rate (mg seed per min)	107.2	29.4	41.2	166.7	84

cone size ( $R = 0.32$ ,  $N = 44$ , one tailed  $p = 0.016$ ) and both of its components: empty cone mass ( $R = 0.32$ ,  $p = 0.017$ ), and seed mass per cone ( $R = 0.32$ ,  $p = 0.019$ ).

For each bout I calculated the feeding rate (mg of seed/min) by multiplying cones chewed per minute of foraging time (including searching and handling), times seed mass per cone. Feeding rate was not correlated with any tree characteristics except a marginally significant result for girth ( $R = 0.26$ ,  $N = 57$  bouts,  $p = 0.047$ ). In contrast, feeding rate was correlated with all cone characteristics. Seed mass per cone explained most of the variance in feeding rate ( $R = 0.74$ ,  $p < 0.001$ ; Fig. 4.1). When the effects of seed mass per cone were removed by partial regression, no other variable was significant. Conversely, the effect of seed mass per cone remained after controlling for any other variable except cone size.

### **Criteria of Tree Selection**

Most feeding bouts were in trees that had been foraged previously, and the cockatoos returned to some trees repeatedly over a period of weeks until they were virtually stripped of cones. Of the 128 bouts observed, 63% were in trees with chewings under them from a previous bout, while the nearest non-foraged sheoak had chewings under it in only 6% of bouts (chi-square = 86.0,  $p < 0.001$ ).

The cockatoos appeared to first choose a tree to sample, and then quickly decide whether it was acceptable or not. The number of cones eaten during a bout had a very bimodal distribution, with the cockatoos eating an average of only 1.8 cones from trees they rejected to forage elsewhere (Fig. 4.2). This decision was also anticipated by the rate of dropping partially eaten cones. At the end of a session, trees that at least one cockatoo had rejected had an average of 43% unfinished cones under them, compared with 14% under non-rejected trees (Mann-Whitney  $U = 184$ ,  $p = 0.004$ ). I addressed separately the questions of how the cockatoos chose trees to sample, and the criteria they used to accept or reject sampled trees.

The cockatoos did not always sample the first tree they landed in, but sometimes moved a short distance to another tree before picking a cone. To examine the criteria for the initial selection of trees to sample, I used only bouts in which neither the foraged tree nor the nearest non-foraged tree had any chewed cones beneath it from an earlier bout. The selected trees differed from the nearest non-foraged tree only in having seeds that were 14% larger on average (paired t-test,  $N = 27$ ,  $t = 1.783$ , one tailed  $p = 0.043$ ). To increase the sample size I compared all trees that showed no signs of having been foraged at any time during the study with those that did. (The latter category included all trees we saw cockatoos eat in, and five “non-foraged” trees with older chewings under them.) Seed size was again the most significant cone characteristic, with a 14% difference ( $t = 2.83$ ,  $d.f. = 124$ ,  $p = 0.005$ ).

To examine the decision to accept or reject a tree after sampling, I compared 26 bouts in which a cockatoo rejected a tree by leaving to forage elsewhere with 90 bouts in which it did not. The only significant difference was that seed ratio was 6% lower in the rejected trees ( $t = 2.17$ ,  $d.f. = 114$ , one tailed  $p = 0.016$ ). The difference was more pronounced in a comparison of trees by preference category. “Preferred” trees had 11% higher seed ratios than “Rejected” trees ( $t = 2.07$ ,  $d.f. = 31$ , one tailed  $p = 0.024$ ), and did

not differ significantly in any other characteristic (Fig. 4.3). Seed size did not differ among preference categories, despite being larger in foraged than non-foraged trees (Fig. 4.4).

The presence of insect larvae did not appear to be a factor in rejecting or accepting trees. The proportion of cone ends per tree-session with signs of insect infestation was unrelated to the proportion that were dropped unfinished ( $R^2 = 0.01$ ,  $p = 0.42$ ). Furthermore, trees rejected by at least one cockatoo during a session did not differ significantly from non-rejected trees in their proportion of insect-infested cone ends (9.8% vs. 6.2%,  $t = 0.75$ ,  $p = 0.46$ ).

### **Consequences of Tree Selection**

To measure the combined effect of all stages of tree selection, I used pairwise comparisons between the foraged tree and the nearest non-foraged tree for each bout in which at least 10 cones were eaten. Foraged trees differed from their non-foraged neighbors in having 23% larger seeds (paired t-test,  $t = 4.44$ , d.f. = 72,  $p < 0.001$ ), 21% more seed per cone ( $t = 4.13$ ,  $p < 0.001$ ), and 14% higher seed ratio ( $t = 4.65$ ,  $p < 0.001$ ). Foraged trees were also much larger than their non-foraged neighbors, with a 70% larger girth and 233% more cones ( $p < 0.005$  for each). Multi-stemmed trees were not represented disproportionately among foraged versus non-foraged trees, or among preference categories (chi-square test,  $p > 0.17$ ). To compare the profitability of foraged and non-foraged trees, I calculated expected feeding rates from the linear regression of observed feeding rate against grams of seed per cone. The expected feeding rate was 13% higher in the foraged trees than in their non-foraged neighbors ( $t = 4.13$ ,  $p < 0.001$ ).

Foraged trees also had higher nutritional quality. Seeds from the pooled sample of foraged trees contained 25.5% more lipid, 9.4% more protein, 17% less fiber, and 12.7% more energy per unit mass than seeds from randomly chosen trees (for each:  $N =$

5, Mann-Whitney  $U = 6$ , one tailed  $p = 0.042$ ). In contrast, there were no consistent differences among the three preference categories of foraged trees (Table 4.3).

Table 4.3. Nutritional content of seeds, expressed as percentage of total mass. Each value represents one measurement of a pooled seed sample.

	<u>Protein</u>	<u>Lipid</u>	<u>Available Carbohydrate</u>	<u>Crude Fiber</u>	<u>Ash</u>	<u>Moisture</u>	<u>Energy (kJ/g)</u>
Foraged drooping sheoak:							
Preferred	22.7	20.7	21.4	23.3	4.4	7.6	15.1
Accepted	21.4	21.3	21.9	22.8	4.7	7.8	15.3
Rejected	22.3	20.1	21.9	23.6	4.4	7.7	15.0
Random drooping sheoak:							
First-year cones	19.9	16.7	22.3	28.8	4.8	7.5	13.3
Second-year cones	20.6	16.3	23.4	27.3	4.7	7.8	13.5
Random slaty sheoak	29.3	17.4	19.1	19.8	7.1	7.3	14.7

### Variation in Individual Feeding Rates

Males fed significantly faster than females, averaging 19% more seed consumed per minute of searching and handling ( $N = 83$  bouts,  $t = 2.87$ ,  $p = 0.005$ ). This was true of the nesting pair (male 28% faster) as well as individuals known not to be nesting (males 18% faster on average). The difference was not attributable to the trees they fed in, as there were no sex differences across bouts in any tree measure (t-test,  $p > 0.3$  for each variable). Rather, males foraged more efficiently, as reflected in both searching and handling times. In paired comparisons of bouts by mated pairs in the same tree at the same time, females spent 5.1 seconds (44%) longer searching for each cone than their

mate (paired t test,  $t = 1.85$ , d.f. = 22, one tailed  $p = 0.039$ ), and 40.4 seconds (23%) longer handling them (paired t test,  $t = 5.66$ , d.f. = 22,  $p < 0.001$ ) (Fig. 4.5).

There was no significant variation in feeding rates between individuals within either sex (ANOVA,  $p > 0.6$ ), and there was no difference between paired and unpaired males ( $t = 0.53$ , d.f. = 51,  $p = 0.60$ ).

## DISCUSSION

### Diet

#### Specialization on *Allocasuarina*

All authors agree that *Allocasuarina* seed is the main food source for the glossy black-cockatoo. Although other food plants are sometimes mentioned (e.g., *Acacia*, *Angophora*, *Eucalyptus*; Blakers *et al.* 1984, Forshaw 1989), such reports are infrequent and no detailed or first-hand accounts have been published. Some observers may have been misled by the cockatoos' habit of chewing bark, wood, or fruits without actually feeding (Pepper 1993, Chapter 3). All published studies have failed to observe glossy black-cockatoos feeding on any food source other than *Allocasuarina* seed cones (Joseph 1982, Clout 1989, Pepper 1993, Chapter 3).

#### Choice of *Allocasuarina* Species

Although the cockatoos exploit several different *Allocasuarina* species, they use only one species as their main food source in any one region; e.g., *A. torulosa* in Queensland, *A. littoralis* in eastern New South Wales and eastern Victoria, and *A.*

*verticillata* in inland New South Wales and South Australia) (Forshaw 1981). This is probably because they exploit only the most profitable species in each area. During the current study the cockatoos had a choice between *A. verticillata* and *A. muelleriana* in the same area. The fact that they fed only on *A. verticillata*, even though their seeds contained less energy and less protein, suggests that feeding efficiency was more crucial than the nutritional quality of the seeds.

Glossy black-cockatoos feeding on different *Allocasuarina* species may differ in the extent to which food quality limits their reproductive success. The few available data suggest that the seed characteristics of *Allocasuarina* species are similar for the same species in different areas. The mean seed size of 3.57 mg reported here is comparable to the value of 3.82 for the same species from Victoria (Withers 1978), and two studies reported similar values for the protein content of *A. littoralis* in New South Wales and Victoria (28.2%, Withers 1978; 27.1%, Clout 1989). In contrast, seed characteristics vary substantially between species. For example, the smaller cones of *A. littoralis* contain a higher ratio of seed mass than *A. verticillata* cones, and their seed contains more protein (Clout 1989).

Because individual trees vary so much in their profitability, the overall quality of foraging habitat probably declines as the best trees are stripped of cones. Because seed production is seasonal, this would produce a substantial seasonal cycle in the quality of the available seed cones. This is true despite the fact that seeds are present year round, and that seed quality does not appear to decline during the first year (Table 4.3). This depletion of the most profitable trees probably explains an earlier episode in which the cockatoos in the study area added slaty sheoak to their diet during several weeks just before the new crop of drooping sheoak cones matured (Pepper 1993).

## Insects as a Possible Food Source

Although South Australian glossy black-cockatoos have only been observed to feed on sheoak seed cones, the question remains whether insects are a significant source of nutrition for the cockatoos. All other black-cockatoos (*Calyptorhynchus spp.*) feed on insect larvae at least occasionally (Forshaw 1989), and in this study 7.7% of chewed drooping sheoak cones showed signs of insect larvae. However, the cockatoos' behavior suggests that they did not seek out insect-infested cones. The (nonsignificant) trends toward selecting trees with fewer infested cones and dropping infested cones at a higher rate suggest that the insects were not actively sought as a food source. *C. l. lathami* feeding on *A. littoralis* also lacked any obvious preference either for or against insect-infested seed cones (Clout 1989). This is in contrast to the behavior of white-tailed black-cockatoos feeding *Banksia* fruits, which feed on seeds but also clearly seek out weevil larvae as a food source (Scott & Black 1981). Despite these negative results, it is still possible that glossy black-cockatoos sometimes seek out insect larvae in seed cones. *Allocasuarina* seed cones host a variety of species from several families, and their food value could vary substantially (Andersen & New 1987).

Forshaw (1989) states that glossy black-cockatoos extract wood-boring grubs from *Allocasuarina* trees, but provides no details. There are no reports of this behavior by *C. l. halmaturinus*, but there is one observation of drooping sheoak trees left with many broken and chewed branches after the cockatoos fed in them, suggesting they may have been extracting larvae from the branches (T. E. Dennis, pers. comm.).

## **Foraging Behavior**

### **Cone Handling**

It is unsurprising that the amount of time required to handle a cone is most closely related to its total mass, but it is worth noting that only 10% of the variance in cone handling times was explained by cone size. This contrasts sharply with Clout's (1989) finding that cone size explained 70% of the variance in handling times of *Allocasuarina littoralis* cones by *C. l. lathami*. Unmeasured factors such as cone hardness may affect handling time much more for drooping sheoak than for *A. littoralis*.

Although I did not attempt to quantify it, the separation of seeds from cones appeared to be quite complete. The fact that some empty, hulled samaras were noted is consistent with a report that captive glossy black-cockatoos split samaras and extract their contents (Sindel & Lynn 1989). Foraging on casuarina seeds thus involves rather complex and rapid manipulations. The entire process of picking the cone, shredding it, separating samaras from the shredded cone, and splitting samaras and extracting their contents, required only 2.0 seconds per seed.

### **Choice of Individual Trees**

Several stages of active choice seem to affect the cockatoos' pattern of tree preference. Past experience is probably important, as most bouts occurred in recently foraged trees even though most trees in the area did not show feeding signs. The tendency to return to favored trees creates a bias toward larger trees, which can be visited more times before their seed supply is exhausted. This is apparently why feeding bouts usually took place in trees that were larger and held more cones than their non-foraged neighbor, even though the initial selection of trees (without signs of prior feeding) revealed no preference for large trees, and larger trees were no more likely to be accepted

after sampling. It is not clear whether the cockatoos use memory, visual cues of past feeding, or both to return to favored trees.

In evaluating trees that had not been fed on recently, the cockatoos appeared to make discriminations at two points. The first was the choice of a tree to sample, which discriminated mainly on the basis of seed size. Although seed size was not the best predictor of feeding rate, it was highly correlated with the trait that was (seed mass per cone), and may have been easier to assess. Seed size may also serve as a cue for nutritional quality. Larger seeds would have a higher ratio of volume to surface area, and thus a higher ratio of nutritious embryo and endosperm to fibrous seed coat. It is not clear how the cockatoos could evaluate seed size before sampling any cones, but seed size might affect the cone's external morphology, and thus provide visible cues.

The second stage of tree selection was apparently based on the additional (non-visual) information gained from sampling one or a few cones from a tree. This suggests that there was much less variation between cones within the same tree than between trees, which is consistent with our unquantified observations and with data on *A. littoralis* (Clout 1989). Tree selection after sampling discriminated mainly on the basis of the seed to cone ratio. This was not an important determinant of feeding rate, but may have affected energy efficiency. Drooping sheoak cones are extremely hard and tough, and shredding them probably requires considerable energy. The ratio of seed to cone mass would reflect the work required to shred woody cone material per gram of seed harvested. The fact that this discrimination occurred only after sampling suggests that seed ratio is not apparent from the cones' external morphology.

Past exposure to fire did not seem to affect trees' profitability relative to others of the same size. Multi-stemmed trees had a relatively narrow size distribution, probably because they had re-sprouted from the base of the trunk after the above-ground parts were killed by fire (Chapter 2). These re-growth trees did not differ from unburned trees in

their cone and seed characteristics, and were not discriminated against by the cockatoos. In contrast, tree size was correlated with the traits the cockatoos preferred, and larger trees did yield a slightly higher feeding rate.

The net effect of the cockatoos' preferences among individual trees was to substantially increase both their rate of seed intake and the nutritional quality of the seeds they ate. The combined effect of the 13% increase in intake rate and the 13.3% increase in energy content amount to a 28% increase in the rate of energy intake. To a first approximation, their tree preferences can be interpreted as a means of maximizing their food intake rate in grams of seed per minute spent foraging. However, some aspects of choice, such as the preference for seeds that are larger, more nutritious, and protected by less woody material, indicate that the cockatoos' behavior optimizes their net rate of energy gain.

The criteria for choosing individual trees used by *Calyptorhynchus lathami halmaturinus* feeding on *Allocasuarina verticillata* in the current study are similar to those of *C. l. lathami* feeding on *A. littoralis* in New South Wales (Clout 1989). The latter study found that the cockatoos sampled a few cones before accepting or rejecting a tree, and that preferred trees had larger cone crops, more and larger seeds per cone, greater seed mass per cone, and higher ratios of seed to cone mass. The results differed in that the ratio of seed to cone mass predicted tree preferences better than total seed mass per cone.

### **Sex Differences in Foraging Behavior**

Males foraged substantially more efficiently than females. This was probably not explained by sexual size dimorphism. Although males tend to be slightly larger than females in the species in general, in a sample of four males and two females from Kangaroo Island males had slightly larger wings and bills but slightly smaller tails and

tarsi (Schodde *et al.* 1993). It also seems unlikely that differences in bill size, ranging from 2 to 7% for various measures, could account for a 23% greater handling efficiency. Instead, males were probably more highly motivated to feed than females. In support of this idea, males were faster at searching for as well as handling cones, and instead of reducing their foraging time to offset their greater efficiency, they actually spent more time foraging per day than females (Chapter 5). One likely reason for their higher motivation is that males often regurgitate food for their mate, especially during the breeding season (Chapter 3). This would not account for relatively high foraging efficiencies in unpaired males, however. Another possible explanation is that during the breeding season males are more active than females (Chapter 5). If males do forage more rapidly than females because their energetic needs are higher, male foraging rates should be lower relative to females outside the breeding season, both because male activity rates drop (Chapter 5), and because they feed their mates less often (Chapter 3).

### **Food Intake and Nutritional Requirements**

Glossy black-cockatoos that were not nesting foraged an average of 6.39 hours per day, while nesting females foraged 2.84 hours, and their mates foraged 6.13 hours per day (based on 104 hours of focal follows during 24 March - 1 May, see Chapter 5). Thus based on the average rate of 107 mg of seed per minute, non-nesting birds ate about 41.2 g of seed per day, and nesting pairs averaged 28.8 g per bird. (The sexes are averaged because males regurgitate food for their mates.) Based on the average values for “Accepted” and “Preferred” trees, this represents 626 kJ of energy and 9.10 g of protein per day while not nesting, and 438 kJ and 6.38 g of protein while incubating.

To compare glossy black-cockatoo’s daily energy intake with the typical energy requirements for birds of similar body mass, I used published equations for daily energy expenditure as a function of body mass based on linear regressions. As an estimate of

body mass, I used the weights of 20 male and 20 female glossy black-cockatoos of unspecified geographic origin reported by Forshaw (1981). Because the sex difference in this sample was less than 2% and sexual dimorphism may reverse between subspecies (Schodde *et al.* 1993), I pooled sexes to produce a mean value of 426 g. The equation of Walsberg (1983), based on 31 bird species that do not forage in flight, with metabolic rates measured by various methods, predicts a daily energy expenditure of 516 kJ/day for a bird of this size. The equation of Nagy (1987), based on 24 non-passerine species measured using the doubly-labeled water method on free-living animals, predicts a daily energy expenditure of 447 kJ/day. The two figures thus agree that the non-nesting birds were eating enough to exceed their expected “typical” metabolic energy requirements, excluding the production of new biomass. A regression equation for protein requirement based on body mass (Robbins 1993) predicts that the cockatoos need 5.10 g of protein per day for maintenance, exclusive of new biomass. The non-nesting birds exceeded this amount by 78%. Thus protein did not appear to be a limiting nutrient for non-nesting birds.

In contrast to the non-nesting birds, the two regression equations agree that incubating pairs were not eating enough to meet their expected metabolic needs, excluding any additional demands of incubation. Nutritional requirements are expected to increase sharply during the nestling stage. According to the regression equations given by Walsberg (1983), the energy requirement imposed by the glossy black-cockatoo’s single nestling would average 202 kJ/day, and peak at 328 kJ/day. Thus even though females forage for longer periods as the nestling stage progresses (*pers. obs.*), this appears to be an extremely energetically stressful period. During the incubation stage the rate of protein intake was only 24% above the expected maintenance level, excluding the production of new biomass. Thus during the nestling stage protein would also very likely be in short supply. These findings suggest that nesting birds may be nutritionally

stressed, and this is consistent with the fact that glossy black-cockatoos are the only member of the genus with a clutch size of only one egg (Forshaw 1989). This may also explain the fact that a survey during the breeding season found that the distribution of glossy black-cockatoos among habitat patches was correlated with the quality of food trees (Chapter 2).

### **Directions for Future Research**

These results suggest that glossy black-cockatoos' energy budgets, and possibly reproductive success, are constrained by the quality of the trees they forage in, and by their efficiency in extracting seeds. Additional factors beyond those included in the current study may influence glossy black-cockatoo nutrition and tree selection. One is the role of secondary compounds. Drooping sheoak produces tannins (Gross 1992), which may be present in the seeds. Concentration of tannins varies between individuals in many plant species, and this could affect the cockatoos' tree preferences. Trace nutrients may also be important. Calcium deficiency is a common problem for glossy black-cockatoos in captivity (Connors & Connors 1988). Lysine is often a limiting amino acid in captive birds, and a study of cockatiel (*Nymphicus hollandicus*) chicks found that it was difficult to meet lysine requirements using diets based primarily on seeds (Grou & Roudybush 1986). Nothing is known about levels of either calcium or lysine in drooping sheoak seed.

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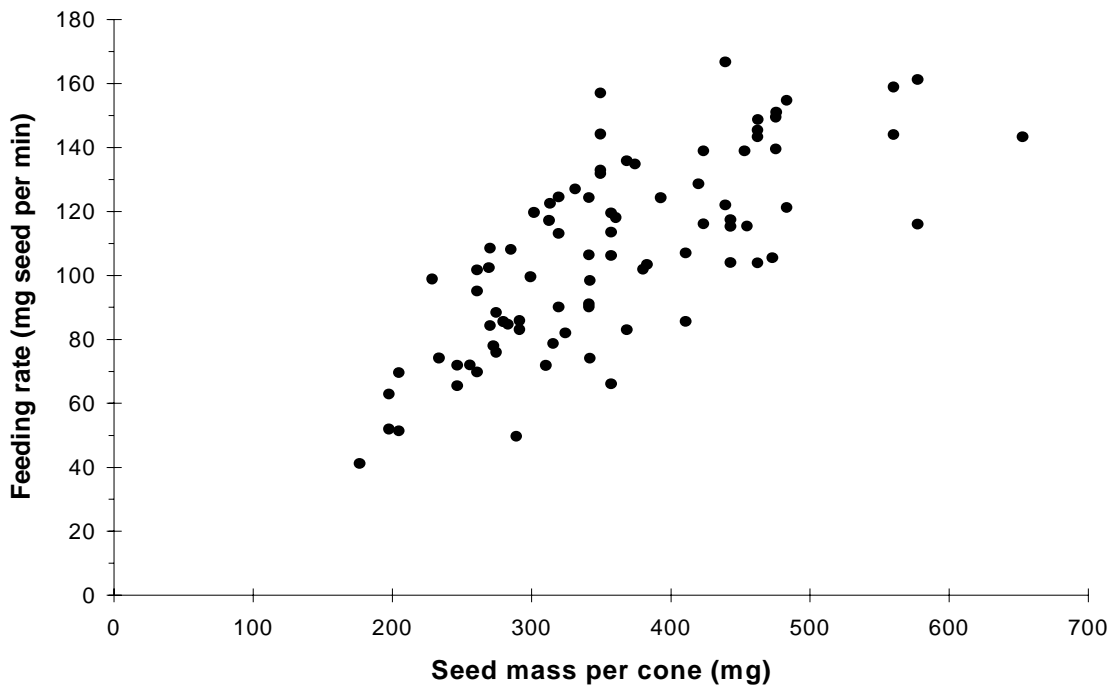


Figure 4.1. Feeding rate versus seed mass per cone.

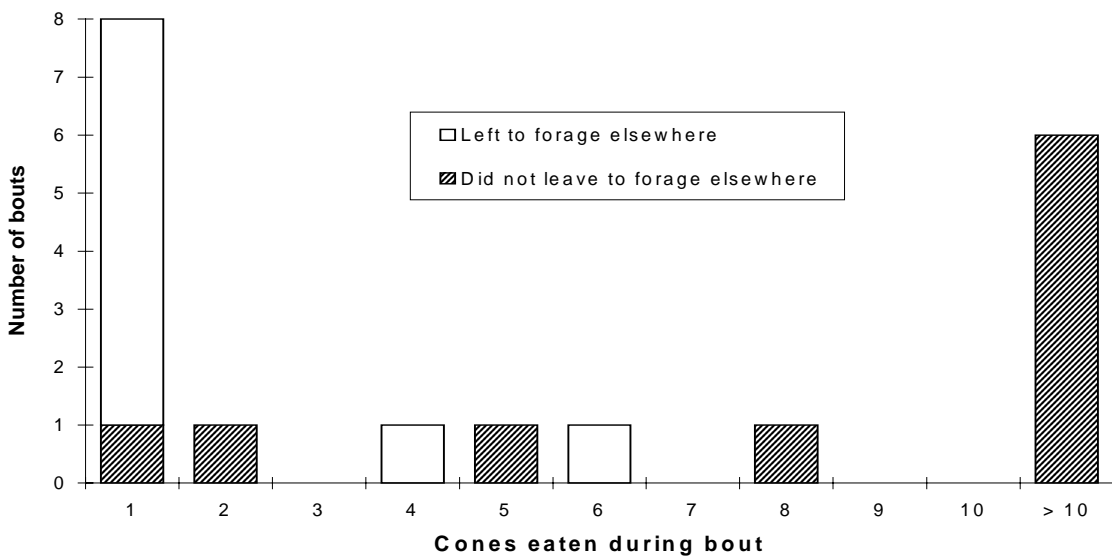


Figure 4.2. Number of cones eaten in bouts in accepted versus rejected trees. Includes only bouts in which both the foraged tree and its nearest non-foraged neighbor had no old chewings beneath them, and in which the total number of cones eaten was known.

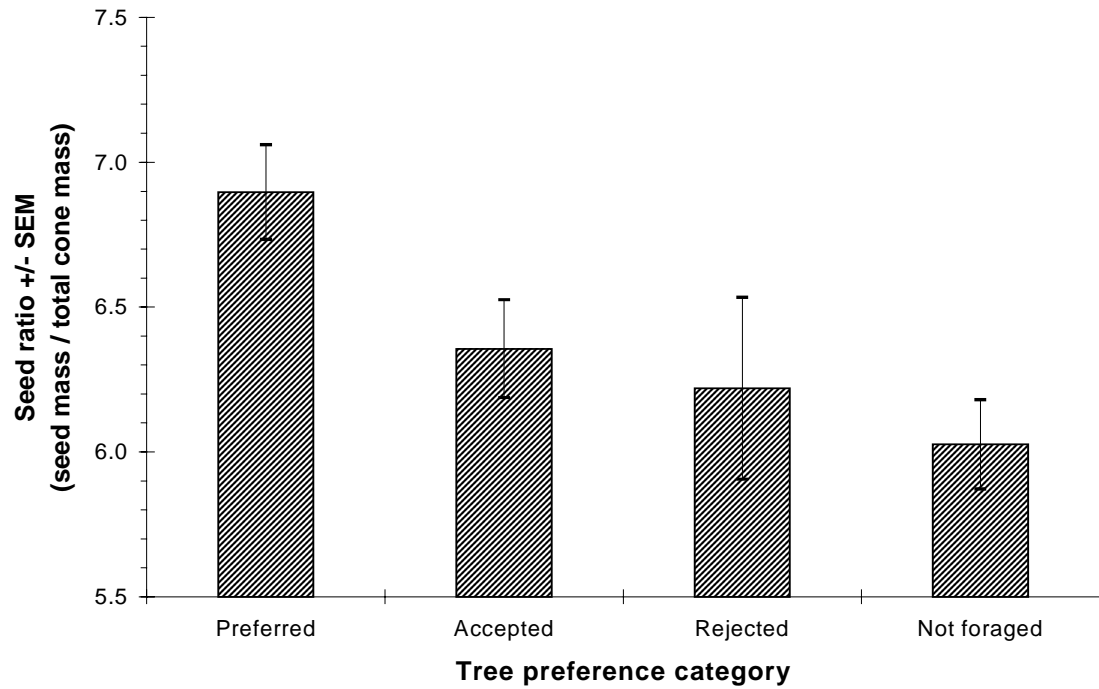


Figure 4.3. Differences in seed ratio between categories of trees.

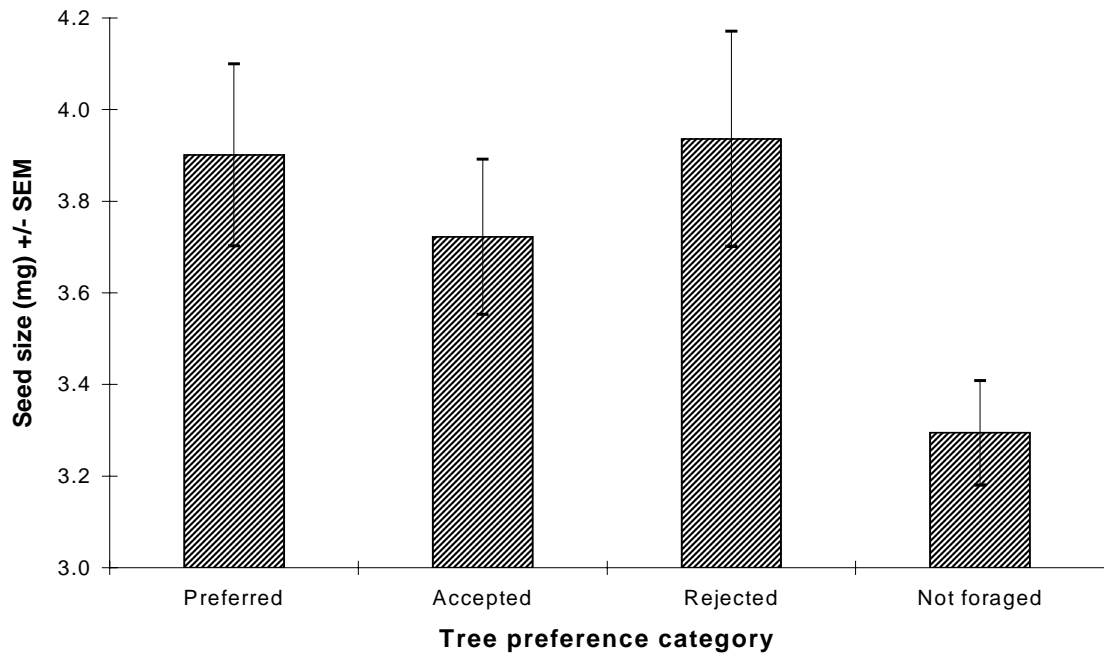


Figure 4.4. Differences in seed size between categories of trees.

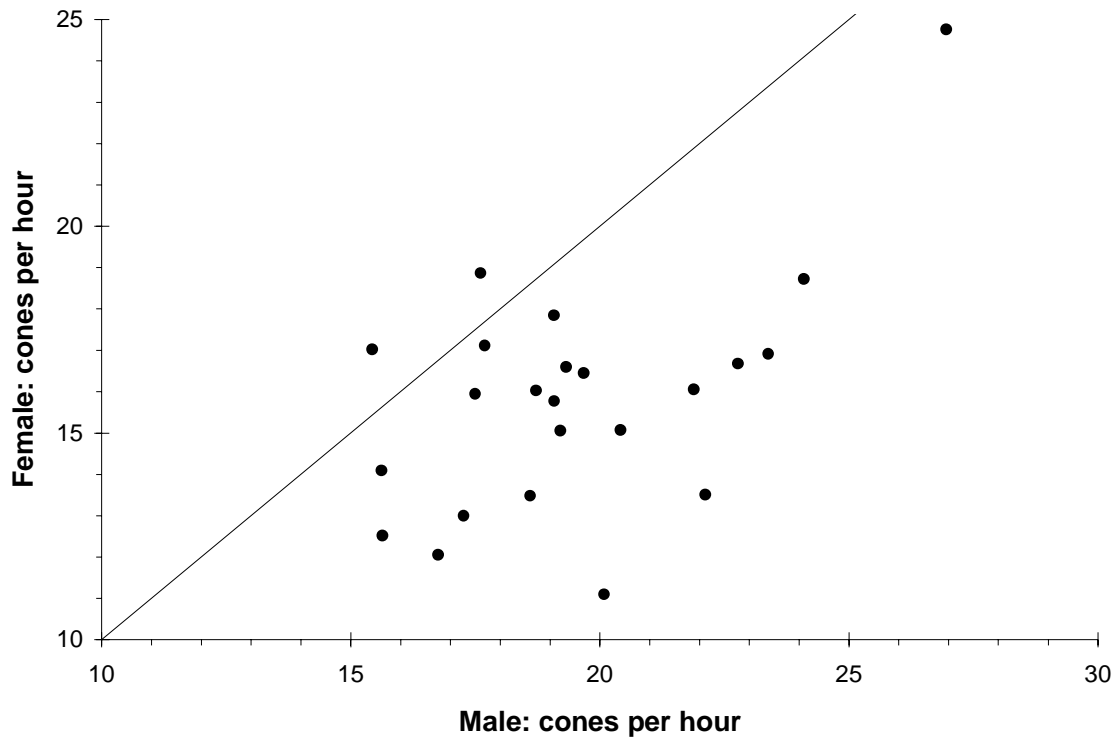


Figure 4.5. Foraging efficiency of females versus males. Each point represents the feeding rates for a mated pair feeding in the same tree, including both search and handling times. The diagonal line indicates equal foraging efficiency for female and male.

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