

WebPanel 1. Model description and parameter estimation

Model structure

Impacts were compared using a deterministic discrete time population model, after Keitt *et al.* (2002). The population size at time t is represented as a vector, $\mathbf{N}(t)$, with six life-stage classes corresponding to the number of individuals in their first, second, third, fourth, and fifth years of life, and those in their sixth year or greater. The number of animals in each of these classes changes according to the matrix \mathbf{M} as

$$\mathbf{N}(t + 1) = \mathbf{N}(t) \cdot \mathbf{M},$$

which describes the stage-specific fecundity (F_{stage}) and mortality ($1 - S_{stage}$) schedules as

$$\mathbf{M} = \begin{bmatrix} & & & & & F_6 \\ S_1 & & & & & \\ & S_2 & & & & \\ & & S_3 & & & \\ & & & S_4 & & \\ & & & & S_5 & \\ & & & & & S_6 \end{bmatrix}$$

As is common in these models, we follow only females in the population and assume a 1:1 population sex ratio. The stage survival probabilities are fairly straightforward to calculate, with each of the n possible mortality sources contributing multiplicatively to the survival probability

$$S_i = \prod_{j=1}^n S_j$$

The fecundity schedule is slightly more complex, as it must account for indirect impacts of adult mortality in the process of laying, brooding, and fledging. The expected per capita contribution of an adult (aged 6 years or more) to the first year class is composed of the probability that a female breeds, p_b , the probability that a female lays an egg, p_e , the probability that an egg successfully fledges, p_f , the probability that both parents survive the reproductive period, S_r , the probability that a fledgling survives its first full year of life, S_0 , and the probability that the chick is female, 0.5, times the clutch size (1 egg).

$$F_6 = 0.5 p_b p_e p_f S_r S_0$$

Demographic parameter estimation

The demographic rates for the model are based on estimates for similar species which have previously been used as proxies for this species (Baker and Wise 2005; WebTable 1). The values were updated based on recent survey work (Priddel *et al.* 2006) on the Lord Howe Island breeding population, which was used to calculate the components of fecundity, and to estimate the potential effects of the various mortality sources. Priddel *et al.* (2006) provide estimates of timing of egg laying, breeding success, and burrow occupancy. To estimate the probability of an

egg becoming a successful fledgling from this breeding success estimate, the data must be adjusted, as these researchers found they had missed some eggs early on and were unable to observe the entire breeding period, missing an expected 28 days at the beginning and 21 days at the end of the breeding season (Marchant *et al.* 1993; Priddel *et al.* 2006). To correct for the missed eggs, we utilize the survival probability of eggs in nests that were relocated (estimated by Priddel *et al.* [2006] as 0.50), which can then be divided into the number of chicks that were found on the second observation that were not observed as eggs, to correct for missed eggs in calculating the proportion of burrows with eggs:

$$\frac{116 \text{ eggs} + \frac{10 \text{ fledges}}{0.5 \text{ fledges egg}^{-1}}}{240 \text{ nests}} = 0.567 \text{ eggs nest}^{-1}$$

From this estimate of the frequency of burrows with eggs, we can estimate the number of fledges per egg, using the estimate of the number of fledges per burrow:

$$\frac{0.27 \text{ fledges burrow}^{-1}}{0.567 \text{ eggs burrow}^{-1}} = 0.476 \text{ fledges egg}^{-1}$$

If we express the probability of transition from an egg to a successful fledgling as a daily survival probability over the observed period (96 days), it can then be extrapolated to the entire breeding period (145 days) to estimate:

$$p_f S_r = \left((0.476)^{\frac{1}{96}} \right)^{145} = 0.326 \tag{A1}$$

Note that this estimate is empirically derived, and includes all sources of mortality that impinge upon breeding success, including predation on eggs and fledglings and mortality of adults due to predation and bycatch. We find the relative contributions from each of these mortality sources, assuming all mortality above the base level comes from either predation by rats or from bycatch. Fisheries bycatch of flesh-footed shearwaters was estimated to be 4783 birds during the 2002–2003 breeding season, which, following Baker and Wise’s (2005) estimate of 75% of the population breeding and a 1:1 sex ratio in the bycatch sample, would yield 1793 birds of either sex killed. Using this number of mortalities and the number of breeding birds of each sex (17 462), the probability of one parent surviving bycatch mortality during a year is 0.8973. Given that we assume a base survival probability of 0.94 for breeding adults (WebTable 1), we take the product of this probability, adjusted for the length of the breeding season, and the probability of surviving bycatch to get a joint probability of surviving all mortality sources in 2002–2003 breeding season of

WebPanel 1. Continued

$$S_r = \left[\frac{17,462 - 0.75 \left(\frac{4,783}{2} \right)}{17,462} \right] \left(0.94^{\frac{5}{12}} \right) = 0.8745$$

We assume rats do not prey on adult shearwaters, and thus ignore this mortality source. Factoring the estimate for S_r out of (A1), we are left with p_f , which must include rat impacts on chicks in the 2002–2003 breeding season. We assume that, in the absence of rats, $p_f = 1$ (ie all mortality in the egg to fledgling stage is due to predation by rats).

Once the demographic rates have been estimated, it is possible to determine a starting population age structure. We used the estimates of the 2003 demographic rates, including a bycatch of 4500 birds, and the estimated rat density under the current control measures, to estimate the stable age structure. All simulations were run starting from this stable age structure.

Mortality response curves and reduction costs

We have to estimate the relationship between the mortality rate and investment in order to evaluate the cost effectiveness of the alternative actions, which implies relating shearwater mortality to the intensity of the impact, and secondly the cost of a unit reduction of the impact across the range of intensity. Starting with the fisheries impact, we first explore the effect of a fishery closure on population dynamics. The goal is to estimate the relationship between the area closed and the expected number of birds caught. We utilized fisheries observer data collected by the Australian Fisheries Management Authority between 2001 and 2005 in the eastern tuna and billfish fishery. We fit three Poisson regression models to the shearwater catch data: a null model assuming only a mean catch (AIC = 1793), a two-component relationship with a mean level and an effect of distance to the breeding colony (AIC = 1500), and a more complex model including year, month, and whether fishing was done in the day or night, in addition to the distance effect (AIC = 966). All of the parameters in the most complex model were highly significant ($P < 0.0001$), and, given its lower AIC value, we chose this model to predict the effect of a fisheries closure of a given size. To do this, we set the remaining parameters at fixed values (year = 2002, month = 11, day = yes), and calculated the expected proportional reduction in catch per unit effort for a closure of a given radius around the breeding colony.

Addressing the full complexity of the cost of a closure including the responses of the fishermen, their markets, and target species, would require a fully integrated economic and biological model, which is currently not available. In the absence of such an analysis, we take a simplified approach, estimating the cost based on the expected change in fish catch. Vessels in this fishery readily move between north and south among ports along Australia's east coast, and thus the

primary axis of differentiation among operators is vessel range, which determines the distance offshore at which they can operate. To determine the cost of a closure, for each vessel we calculated the percentage of all sets deployed during 2003 that were east of the closure area (ie further offshore than the offshore edge of the closure area) and the percentage that were west of the closure area (ie inshore of the closure area). The effort by the vessel that would have occurred in the closed area was then allocated to the inshore and offshore regions in proportion to this historic use, and assigned the average CPUE of the target species in those areas based on fisheries logbook data provided by the Australian Fisheries Management Authority. The cost of a closure was determined by the difference in the expected catches by the vessel in the closed area versus the area(s) to which its effort is reallocated. The value of the catch was calculated based on the average values paid on the Sydney Fish Market (www.sydneyfishmarket.com.au). It is important to note that this approach ignores the potential negative effects of overfishing and competition between vessels with the reduction in the size of the fishing grounds. Conversely, it also ignores any recovery or spillover effects that could occur with the closure.

With respect to the impact of rats, we estimated the consumption of shearwater eggs and fledglings by a rat based on its daily caloric requirements. We calculated food intake in grams, b , based on metabolic rates using the allometric relationship,

$$b = 3.32 * (\text{predator weight})^{0.774} * \frac{2.86}{18}$$

and reported rat weights (212 grams) from islands (Nagy 1987). We assumed a rat in the breeding colony meets 100% of its daily metabolic requirements from seabird eggs and chicks, when available (Nagy 1987). Furthermore, we assumed a rat can consume 100% of an egg and 100% of the edible portion (50% by weight) of a shearwater carcass as estimated by Keitt *et al.* (2002). Breeding phenology (62 days from laying to hatching, 90 days from hatching to fledging) and egg weight (75 grams) were based on data for flesh-footed shearwaters (Marchant *et al.* 1993), while daily weight gain (73% of adult mass at hatching, 140% of adult mass at maximum weight, and 106% of adult mass at fledging) was taken from a study on short- and wedge-tailed shearwaters feeding in the same region (Schultz and Klomp 2000). Taking these data together, we estimate a rat will consume 63 shearwaters during the 152 day brooding season.

There are no data available on current rat densities in the breeding colonies; however, using the estimate of 63 shearwaters consumed per rat, a colony area of 17 462 pairs covering 24.3 ha, $p_f = 0.378$ (implying 63.6% of eggs and fledglings die), and with the assumption that all egg and chick mortality is due to rats, we estimate the density of rats on the breeding colony is 7.25 rats per ha. This agrees with historic estimates of rat density; Miller and Mulette (1985) used snap traps (which kill trapped animals) and trapped 3–4 animals in 3 nights on a grid

WebPanel 1. Continued

of 50 traps covering 0.56 of a hectare within the poison baiting area. Scaling up, this would yield a lower estimate of roughly 6–8 rats per ha, in rough agreement with our estimate based on the shearwater mortality. Natural rat densities are held at this lower level with an ongoing investment of US\$39 000 per year in poison baiting for the control of rat impacts on economically valuable palms (Parkes *et al.* 2004). Estimates of rat density in uncontrolled areas range from 12 to 68 caught in snap traps on a 50-trap grid covering 0.56 ha, for an average estimate across the five sites and two years of sam-

pling of 48 rats per ha (Miller and Mullette 1985). The response of rat density to investment in control is estimated by assuming a logarithmic relationship between investment in poisoning and rat density. Taking our more conservative metabolic estimate of rat density in 2003 under control measures, the log of rat density is reduced by -0.000038 rats ha^{-1} dollar invested¹, from a maximum of 48 rats ha^{-1} . The cost of a complete eradication of rats, US\$500 640, was based on the current cost–benefit study for the Lord Howe Island Management Board (Parkes *et al.* 2004).

WebTable 1. Demographic rates used in the population model

Parameter	Value	Source	Species
S_0 ¹	0.96	Baker and Wise 2005	short-tailed and sooty shearwater
S_1 – S_5 ¹	0.80	Baker and Wise 2005	short-tailed and sooty shearwater
S_{6+}	0.94	Baker and Wise 2005	short-tailed and sooty shearwater
p_b	0.75	Baker and Wise 2005	short-tailed and sooty shearwater
p_e	1	assumed	flesh-footed shearwater
p_f	$0.378 - I^2$	Priddel <i>et al.</i> 2006	flesh-footed shearwater
S_r	0.875	estimated	flesh-footed shearwater

¹Calculated based on the annual survival estimate of prebreeders, adjusted to cover the period from fledging (age 10 months) to first birthday

²Dependent on rat density; varies from 1 in the absence of rats to 0.378 at current control levels