Demographic Forecasting in Koala Conservation

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Abstract: *The koala currently needs conservation intervention. There is clear evidence of decline in many populations, but the existence of other stable or expanding populations offers the possibility of a variety of creative solutions to their conservation problems. The 1998 National Koala Conservation Strategy emphasizes the need to obtain demographic information and to use this information to assess management options for koalas. We need accurate diagnoses of the status of koala populations and forecasts of their demographic future with and without particular management actions. In a qualitative fashion, this process has been undertaken many times on a local and national scale. Quantitative demographic forecasting tools are increasingly available, and koala management could benefit from their application both at the scale of individual populations and more broadly. There is already a considerable body of suitable data on the dispersal, effects of normal and catastrophic environmental variation on reproduction and survival, and on the effects of habitat change. Demographic forecasting, however, is hampered because the full suite of information is rarely available from a single population. In two Queensland populations, retrospective population viability analyses provided forecasts that were in agreement with observed population trends. Work is needed to determine whether data from one population can be applied to other populations. Models can then be developed to make projections at a multipopulation level on the basis of local population dynamics and dispersal. Certain koala populations, because of their long history of study, offer the opportunity to test demographic models retrospectively. These tests will not only aid in fine-tuning the models for koala biology and data but will also assist with the more general process of validating the models.*

Predicción Demográfica de la Conservación del Koala

Resumen: *Actualmente, el koala necesita intervenciones de conservación. Existen pruebas claras de una disminución en muchas poblaciones, pero la existencia de otras poblaciones estables o en expansión ofrece la posibilidad de una diversidad de soluciones a los problemas de conservación. La estrategia de Conservación Nacional del Koala de 1998 pone énfasis en la necesidad de obtener información demográfica y usar esta información para evaluar las opciones de manejo para los koalas. Necesitamos diagnósticos precisos de la situación de las poblaciones de koalas y predicciones de su futuro demográfico con y sin acciones particulares de manejo. De una manera cualitativa, este proceso se ha llevado a cabo muchas veces a escala local y nacional. Las herramientas para la predicción demográfica son cada vez más viables y su aplicación podría beneficiar el manejo del koala tanto a nivel de poblaciones individuales como a un nivel más amplio. Existe un considerable cuerpo de datos sobre la dispersión, los efectos de la variación ambiental normal y catastrófica sobre la reproducción y sobrevivencia y los efectos de cambios en el hábitat. Sin embargo, es difícil hacer predicciones demográficas ya que es raro que toda la información provenga de una población única. En dos poblaciones de Queensland, análisis retrospectivos de viabilidad poblacional suministraron predicciones según las tendencias poblacionales observadas. Se necesita más trabajo para establecer si los datos de una población pueden ser aplicados a otras poblaciones. Se pueden desarrol-*

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lar modelos para realizar proyecciones a nivel multi-poblacional en base a la dinámica y la dispersión poblacional local. Ciertas poblaciones de koalas ofrecen la oportunidad de evaluar modelos demográficos retrospectivamente debido a su larga historia de estudios. Estas pruebas no solo permitirán ajustar los modelos de la biología de koalas y los datos, sino que ayudarán también en el proceso más general de validación de los modelos.

Introduction

The best time to consider conservation management is before the population has become so small that options are limited. The koala is currently at an appropriate point for conservation intervention: there is clear evidence of decline in some populations, but the existence of other robust populations in diverse locations offers the possibility of a variety of creative solutions to their conservation problems (Melzer et al., this issue). Evidence of genetic and morphological differentiation on a north-south axis highlights the importance of maintaining populations throughout the range (although all populations appear to belong to a single evolutionarily significant unit; Houlden et al. 1999; Sherwin et al., this issue). Unfortunately, the koala faces different conservation problems in each part of its range. Even apparently secure populations may have poor long-term prospects because of intrinsic factors such as low genetic variation or extrinsic factors such as ongoing habitat loss (Melzer et al., this issue; Sherwin et al., this issue). The northern part of the range appears relatively secure, but processes are underway that could cause conservation problems in the future. In the central part of the species' range, declines are continuing, largely as a result of habitat loss. In the southern part of the range, overhunting led to many severe declines in the 1800s and early 1900s. As a result of relocations, the southern part of the range appears secure for the present, and indeed has expanded relative to the time of European settlement (Melzer et al., this issue). However, southern populations have low genetic variation (Sherwin et al., this issue), so this region may not have good long-term conservation prospects. Also, some introduced island populations in the southern part of Australia are overabundant (Melzer et al., this issue). Although there are numerous koala populations in various conditions, we cannot be complacent about this species because there may be thresholds of habitat loss beyond which sudden extinction occurs (Hanski 1998). It has also been suggested that disturbed populations such as the koala may not be at equilibrium but may be carrying an "extinction debt" (Tilman et al. 1994) that predisposes them to sudden extinction. Tilman et al. (1994) believe that abundant species such as the koala are particularly susceptible to the extinction debt, but this assertion depends on assumptions about the relationship between abundance, competitive ability, and dispersal (McCarthy et al. 1997).

The National Koala Conservation Strategy has identified the need for more powerful and reliable methods of demographic forecasting (Australia and New Zealand Environment and Conservation Council [ANZECC] 1998). Demographic forecasting can assist koala conservation in three ways: assessment of status at local and national levels and evaluation of management options. Proper management of koalas requires agreement on their status, yet these animals are the subject of a variety of official status designations and public perceptions, in part because of dispute over population sizes, trends, and threats (Melzer et al., this issue). There are various ways to evaluate the conservation status of species and rank their priority for management (Millsap et al. 1990; Mace & Lande 1991; Master 1991; McClanahan & Wolfe 1993; World Conservation Union 1994). One important concept is triage (McIntyre et al. 1992), whose aim is to direct resources to species that have begun to suffer conservation problems yet are capable of responding to management actions. Thus it is important to diagnose which apparent threats are actually causing population decline and whether achievable management actions will arrest the decline. To provide a sound basis for the discussion of status and to evaluate our ability to alleviate the threats, it is necessary to forecast the likely future of koala populations with and without management of particular threats—population viability analysis (PVA; Shaffer 1981; Gilpin & Soulé 1986). Although assessment of the conservation status of an entire species implies the ability to forecast the likely future of the whole species, explicit predictions are rarely made on this scale. Computer models have been developed to make demographic projections for many species (e.g., Lacy & Clark 1990; Maguire et al. 1990; Haig et al. 1993; Possingham et al. 1993; Hanski 1994; Bradstock et al. 1996; Akçakaya & Atwood 1997). Before PVA is used to assess threats to a species or guide development of a conservation strategy, it is important to evaluate whether the data are sufficient to provide useful population projections. It is also important to examine the validity of the chosen model for the target species by testing model results against historical data (Brook et al. 1997; Lindenmayer et al. 2000) or by comparing the performance of multiple models (Brook et al. 1999), but this testing has rarely been undertaken (Mills et al. 1996; Brook et al. 1997; Mann & Plummer 1999).

To make demographic forecasts for the entire range of koalas would be a major undertaking because this species' range includes multiple populations scattered over thousands of kilometers. Disparities across this range necessitate careful consideration of the appropriate scales for data collection, analysis, and management. We discuss the likelihood of producing adequate models for forecasting koala population trends at various levels and for evaluating alternative management options in koalas. We discuss the adequacy of koala data for these models and the potential for forecasting methods to be tested and applied in koala management, including a trial of the methods in two populations. Addressing these issues in koala conservation provides a step toward testing the generality of methods for demographic prediction.

Threats and Their Management in Koalas

Conservation modeling should reflect the biology of the species, processes that threaten it, and possible ways to mitigate these threats. It usually involves assessment of the effect of these threats and management actions on mortality, fertility, and other modeled parameters. Currently, the main factors propelling declines appear to be habitat loss, fragmentation, and degradation (Melzer et al., this issue). Net loss of habitat permanently decreases carrying capacity. Fragmentation of the habitat has two main effects. First, it is likely to hinder dispersal, thus reducing the chance of recolonization of patches in a metapopulation and the exchange of genetic information. Second, fragmentation exacerbates other adverse processes, especially edge effects, which in the case of koalas include fire, weeds, dogs, and cars (Melzer et al., this issue).

Although pressures on koalas have changed, it is not always clear what the net effect on model parameters such as mortality and fertility will be. For example, sources of koala mortality have changed dramatically throughout the last 200 years. For thousands of years, koalas experienced mortality from Aboriginal hunting. During the 1800s, intense hunting by Europeans is thought to have been the main cause of decline in the southern part of the koala's range (Melzer et al., this issue). In recent decades, considerable koala mortality appears to be caused by road traumas (Lunney et al. 1996) and dog attacks. Dog attacks may have increased recently and are probably often underestimated because koalas killed by dogs are rarely found unless they were radiocollared (D. Lunney, unpublished data). Other threatening processes, including fire, drought, and possibly reproductive disease, have occurred over long evolutionary times, but their incidence may have varied over time. Forest crown fires can cause high koala mortality, and droughts reduce survival or breeding and may have their greatest impact on young koalas in marginal habitat (Gordon et al. 1988; Melzer et al., this issue). Reproductive disease and consequently lowered fertility is seen in many populations (Melzer et al., this issue; Sherwin et al., this issue). Some strains of this disease may be native to koalas, but some seem to have been introduced recently via contact with domestic animals (Sherwin et al., this issue) and may have adverse effects. On the other hand, disease-free populations sometimes overbrowse their food supply and then crash (Martin 1985*a*,1985*b*), and this pattern may be exacerbated by habitat fragmentation that hinders the movement of koalas and their parasites.

To assess the likely effects of management actions, one needs to know the current status of koala populations and to model the effect of particular management scenarios. Some local management plans are now sufficiently advanced to allow this modeling (Lunney et al. 1999, this issue). Local, state, and national jurisdictions have initiated or suggested a variety of management options, including habitat reservation, habitat regeneration, corridors between habitat patches, dog controls, modification of fire and forestry management, and, for overabundant populations, culling, relocation, or fertility control (ANZECC [Australia and New Zealand Environment and Conservation Council] 1998). Some of these options are being attempted, such as planning controls and tunnels under roads in New South Wales and sterilizing and relocating koalas in South Australia and Victoria (Melzer et al., this issue).

Demographic Forecasting Methods

Population viability analysis can be performed at several levels, including qualitatively or quantitatively and on single or multiple populations. Many qualitative forecasts have been made for koalas on local and national scales (Lunney et al. 1990; Maxwell et al. 1996; Lunney & Matthews 1997; ANZECC 1998; Melzer et al., this issue) but quantitative modeling has not been attempted.

Quantitative forecasting for a single population requires substantial data, including mortality, fertility, and their variation due to chance and interaction with other factors such as the environment, population density, threat processes, and management actions (Lacy 1993; Possingham & Davies 1995; Akçakaya & Atwood 1997). In koalas, fertility can be assessed by counting females with back-young. Absolute mortality rates can be obtained only by extremely intensive studies, but relative mortality rates for different age classes can be assessed by comparing tooth-wear classes (Gordon 1991) of living individuals and skulls found in the same locality. Based on this type of data from Springsure in central Queensland (Melzer 1995; Table 1), the mortality of adult males >3 years was estimated to be 1.15 times higher than that of juvenile males, and the mortality of adult females >2 years was estimated to be 0.53125 times lower than that of juvenile females. This method has its drawbacks. First, it is accurate only if the population is in demographic equilibrium; second, it provides only relative estimates. These relative mortality rates can

Table 1. Numbers of living and dead koalas of different age classes for Springsure in central Queensland.[a]

Sex	*Tooth wear class*[b]	*Number alive*	*Number dead*
Male	2+3	7	7
	>3	27	31
Female	2	2	4
	>2	32	34
Total		34	38

[a] *Data from Melzer (1995).*
[b] *Gordon 1991.*

be converted to absolute rates by comparing the observed age structure with that predicted by preliminary PVA modeling. Based on the assumptions that the population is at equilibrium and all other input is correct, mortality values can be adjusted to minimize departure between observed and predicted age structures while the relative rates of adult and juvenile mortality calculated from field data are maintained. The effect of density on reproduction and mortality is often summarized as the carrying capacity, *K*, which can also be difficult to estimate. A dense population for one part of the koala's range would be a sparse population in another, so *K* cannot be assumed unless through observation of a population crash due to overbrowsing (Martin 1985*b*; Melzer et al., this issue).

An important part of PVA is the estimation of variability in demographic parameters and the association (or otherwise) of these parameters with particular environmental fluctuations. Long-term data sets are vital because diseased populations of koalas can show major fluctuations in fertility (Martin 1981). In the northern part of the range, Gordon et al. (1990*a*) showed that determinants of population size may include habitat quality, disease prevalence, and climatic fluctuations. Koalas consistently occur at different densities in different habitats. If these populations are in equilibrium, the density differences indicate that habitat quality may affect demography. Reduced fertility due to Chlamydial infection and elevated mortality due to prevalence of cystitis are reflected in low growth rates in some populations (e.g., Oakey; Gordon et al. 1990*a*). At Springsure, rainfall strongly influences population size through its effect on dispersal (Gordon et al. 1990*a*). At Mungalalla Creek in western Queensland, a heatwave that caused leaf death in food trees resulted in catastrophic mortality (Gordon et al. 1988). Leaf death was also influenced by moderate drought conditions that prevailed at the time. Mortality during the heatwave varied with habitat quality; it was much lower in better habitat. The severe mortality may also have been a result of an earlier increase in numbers and expansion into poorer habitat where animals were at much greater risk, with the better habitat forming a refuge.

A variety of computer programs is available to assist with the task of predicting trends in a single population (e.g., VORTEX [Lacy 1993], RAMAS [Ferson 1994], and ALEX [Possingham & Davies 1995]). They differ in ways that may affect their application to particular species, including input, simulation method, type of forecast, and provision of error estimates (Lindenmayer et al. 1995; Brook et al. 1999). For example, few programs allow incorporation of the effects of inbreeding on reproduction and survival, although this may be an important factor for koalas (Sherwin et al., this issue). Also, some packages provide no error estimates, which is undesirable because a manager cannot use the standard deviation to gauge the range of possible trajectories for a population managed in a particular way, and because the model cannot be validated by comparison with field data unless the standard error is known.

Data for demographic modeling are often woefully incomplete, so it is necessary to perform tests to determine whether the model works well despite poor data. Unfortunately, the models have rarely been tested against actual population trends for any species (Mills et al. 1996; Brook et al. 1997; Lindenmayer et al. 1999), and although the modeling methods are framed in generally applicable terms, the testing has not been sufficiently broad to assure general validity. Various tests can be performed, ranging from limited validation against a small number of data points to comprehensive tests. To avoid circularity, these tests should isolate the data sets for testing from those used to establish the predictive model. For example, having two data sets from different years allows retrospective tests of PVA models (Brook et al. 1997, 1999). These tests not only aid in gearing the models to a particular species' biology and data, but they also contribute to the more general process of validating the models.

Some koala populations have been studied extensively (Table 2) and offer the opportunity to divide data sets and run retrospective tests. Two examples are from Oakey (southeastern Queensland, 1971–1997) and Springsure (central Queensland, 1976–1997) (Gordon et al. 1990*a*, 1990*b*; Melzer 1995). From these data, one of us (A.P.) estimated parameters for input to VORTEX (version 7.41, Lacy 1993; Table 3). We assumed that there was no inbreeding depression, no density-dependence of breeding, and no correlation between environmental variation of reproduction and mortality. Breeding commences at 2 years in females and at 3 years in males; the maximum age was set to 12 years. The program produced predictions of population size close to the observed values (Fig. 1). The only graphed data used in making the forecast was the initial population size (first point on each graph). Over the modeled period (Fig. 1), Oakey had a probability of extinction (*E*) of 0.380, with further decline predicted over the next 10 years. At Springsure, *E* was 0.063 over the modeled period, so, this population seems secure for the immediate future. Similar results were obtained from RAMAS/stage (version 1.4, Ferson 1994).

Table 2. Long-term koala data sets that could be used as input for PVA modeling.

Population/citation[a]	Density[b]	Trends in abundance	Disturbance[c]	Reproductive data (date)	Survival data (date)
Queensland					
Blair Athol (1)	moderate	stable	−	yes (1994–1998)	yes (1994–1998)
Springsure (2,3)	moderate	stable	−	yes (1976–1997)	yes (1976–1997)
Mt. Zamia (2)	low	stable	−	yes (1990–1995)	yes (1990–1995)
Daisy Hill/Logan/Redlands (4)	moderate	stable/slow decline	+	yes (1996–1998)	yes (1996–1998)
Oakey (3)	moderate	decline	−	yes (1971–1997)	yes (1971–1997)
New South Wales					
Campbelltown (5)	moderate	increase?	+	yes (1991–1998)	yes (1991–1998)
Iluka (6)	moderate	decrease	+	yes (1990s)	yes (1990s)
Bega (6)	low	decrease	−	minimal	minimal
Gunnedah (6)	high	increase	−	yes (1990s)	yes (1990s)
Coffs Harbour (6)	high	decrease	+	yes (1990s)	yes (1990s)
Pt. Stephens (6)	moderate	decrease	+	minimal (1990s)	yes (1990s)
Pt. Macquarie (7)	moderate	decrease	+	yes (1990s)	yes (1990s)
Victoria					
French Island (8)[d]	high	fluctuate, cull	−	yes (1980s)	yes (1980s)
S. Gippsland (8)	moderate	no	−	yes (1980s)	yes (1980s)
Rotamah Island (9)[d]	high	fluctuate	−	yes (1988, 1992–1995)	yes (1988, 1992–1995)
South Australia					
Kangaroo Island (10)[d]	high	increase, cull	+	yes (1997–1998)	yes (1997–1998)

[a] *Data sets largely unpublished, but some published summaries are available: (1) F. Carrick, Ellis et al. (personal communication); (2) Melzer (1995); (3) Gordon et al. (1990*a*, 1990*b*); (4) F. Carrick (personal communication), G. Gordon (unpublished data); (5) Close & Phillips (personal communication); (6) D. Lunney (unpublished data and references in this paper); (7) Wilkes (personal communication); (8) Martin (1981, 1985*a*, 1985*b*), Martin & Handasyde (1991), Mitchell (1989), Mitchell & Martin (1991); (9) Mitchell (personal communication), Martin & Mitchell (1988); (10) B. St. John (personal communication).*
[b] *Density level on a national scale; thus, the Queensland populations are almost all rated as moderate in density, although some are densely populated by Queensland standards (1–2 individuals/ha). Density comparisons are only approximate because some habitats are two-dimensional, whereas others are linear along watercourses or roadsides.*
[c] *Virtually all koala populations have been disturbed by European activities in the last 200 years; the recent intensification of disturbance is coded as (−) no change in disturbance levels or (+) increase in disturbance since 1990, such as progressive land clearing or changes in relocation regimes leading to a nonequilibruim situation for modeling.*
[d] *Artificially established populations.*

Sensitivity analysis allowed us to explore the effect of alterations of different parameters and to investigate the consequences of measurement errors or alteration related to management or threats (McCarthy et al. 1995; Wisdom & Mills 1997). In the Oakey and Springsure koala models, we determined the sensitivity of the output (E and growth rate, λ) to small changes in four parameters: fertility, mortality, inbreeding depression, and correlation between reproduction and mortality. Varying the effect of inbreeding in koalas from zero to the median mammal value of 3.14 lethal equivalents (Ralls et al. 1988) had minimal effect on the results (data not shown). Introducing correlation between the effects of environmental variation on reproduction and survival also did not greatly affect the results (data not shown). The probability of extinction and the growth rate of the populations were more affected by small changes in fertility than by comparable changes in mortality (Table 4). A 10% increase in the fertility rate increased the growth rate from 0.930 to 0.943 at Oakey and from 1.034 to 1.052 at Springsure and decreased E from 0.464 to 0.321 at Oakey and from 0.084 to 0.046 at Springsure. Small changes in the mortality data had a greater effect on the final probability of extinction than on the growth rate of the population. The forecasts were most sensitive to changes in adult mortality and least sensitive to juvenile mortality (Table 4). It therefore appears important to measure fertility and adult mortality accurately and to manage any threats that affect these factors. It would not be wise, however, to devote extensive resources to measuring male mortality because, at least for one New South Wales population, predictions of probability of extinction and final population size are not significantly affected by five-fold differences in values for adult male mortality (L. Carroll et al., personal communication).

The accuracy of these recommendations depends on the adequacy of the modeling process, so testing is important. There are, however, a number of limitations to the type of model testing we describe. First, one must be sure that population fluctuations and trends against which the model is tested are due to the growth rate of the local population, not to mass immigration and emigration, which apparently occur in koala populations during drought conditions (Gordon et al. 1988). Second, in a time series (Fig. 1), the successive points are necessarily correlated with one another unless the population trajectory is completely random. Therefore, the agreement between the final population size and the pre-

Table 3. Values used as input for simulations of koala populations at Oakey and Springsure.

Variable[a]	*Oakey (SD)*[b]	*Springsure (SD)*[b]
Maximum age	12	12
Sex ratio (proportion males)	0.5750	0.5330
Litter size 0 (%)	57.00 (±17.85)	31.00 (±15.61)
Litter size 1 (%)	43.00 (±17.85)	69.00 (±15.61)
Female mortality at age 0	32.5 (±3.25)	30.00 (±3.00)
Female mortality at age 1	17.27 (±1.727)	15.94 (±1.594)
Adult female mortality	9.17 (±0.917)	8.47 (±0.847)
Male mortality at age 0	20.00 (±2.00)	20.00 (±2.00)
Male mortality at age 1	22.96 (±2.296)	22.96 (±2.296)
Male mortality at age 2	22.96 (±2.296)	22.96 (±2.296)
Adult male mortality	26.36 (±2.636)	26.36 (±2.636)
Probability of catastrophe	0.05	0.05
Severity, reproduction[c]	0.550	0.550
Severity, survival[c]	0.630	0.630
Percent males in breeding pool	50.00	50.00
Start at stable age distribution	yes	yes
Initial population size	46	20
Carrying capacity, *K*	70 (±7)	60 (±6)

[a]*The fertility rates averaged over the years 1971–1982 at Oakey and 1976–1982 at Springsure. Mortality rates calculated as described in the text.*
[b]*Standard deviation (SD) due to environmental variation.*
[c]*The multipliers for reproduction and survival in catastrophe years.*

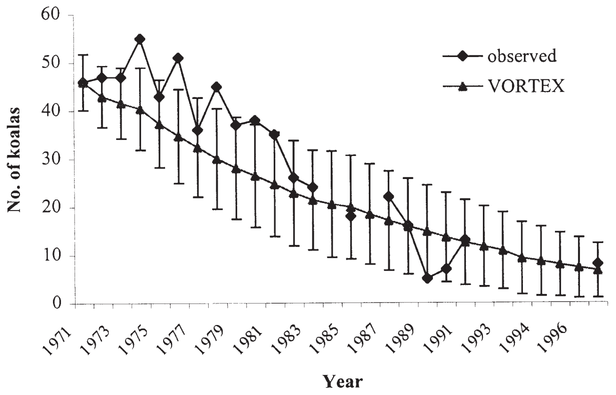
dicted final size in each graph can be interpreted as one point of confirmation of the model, but agreement at other points is not independent confirmation. Finally, conservation managers are often most concerned with the probability of extinction (*E*) rather than the population size or growth rate, so it is necessary to test the predictions of *E.* Testing requires data on the presence and absence of populations under particular conditions. For all these reasons, comprehensive testing of PVA requires modeling of multiple populations and the dispersal among them—metapopulation modeling (Hanski 1994, 1998).

As well as being important for testing of PVAs, metapopulation models may broaden forecasts beyond a single population, as required for assessment of the status of an entire species, such as the koala, whose range includes multiple populations. Although scientists are often reluctant to make these broader forecasts, they are being made by others, so it is useful to examine what part metapopulation modeling could play in the process. It can be difficult to parameterize metapopulation models, and although they have been applied with success in some species, others species have been difficult to model in this way (Hanski 1994; Lindenmayer et al. 1999). Metapopulation modeling requires information on local extinction (which can be derived from single-population modeling), dispersal between populations (which may delay extinction or allow recolonization), and the nature of habitat loss or gain.

Rates of exchange among populations can be estimated by genetic methods and by marking or radiotracking studies, but each method has limitations (Sherwin & Murray 1990). Genetic estimates incorporate a time lag, so they are liable to tell us the average rate of genetic exchange some generations ago. In recently disturbed populations such as koala, this rate may not be a reflection of long-term averages or of current dispersal (Sherwin et al., this issue). Tagging and tracking methods can tell us what genetic exchange is currently occurring, but only for those rare studies that are sufficiently extensive in area and time to yield a good estimate of the proportion of dispersing animals that actually survive and breed. Given the limitations of genetic and nongenetic methods for detecting dispersal, the two must be used in conjunction with each other.

Populations that are relatively demographically independent "management units" (Moritz 1994) have been identified within the range of koalas (Houlden et al. 1996; Sherwin et al., this issue) so a metapopulation model would be appropriate in their case. The number of these units and their boundaries, however, have not been identified. On a finer scale (<100 km), other models may be appropriate for koalas, including a continuous model in which there are no discrete units, or a source-sink model in which some koala populations are transient (i.e., periodically recolonized from a permanent source). There is evidence that the latter model applies to some Queensland populations because during drought koalas appear to congregate in areas of better habitat quality (Gordon et al. 1988). Thus, the effect of a given level of dispersal depends on whether the dispersing individuals are able to readily detect high-quality habitat and remain there (Tilman et al. 1994; Lindenmayer et al. 1999). Artificial relocation of koalas must also be considered in metapopulation models.

Many koala conservation problems stem from habitat loss and fragmentation, so the size and shape of rema



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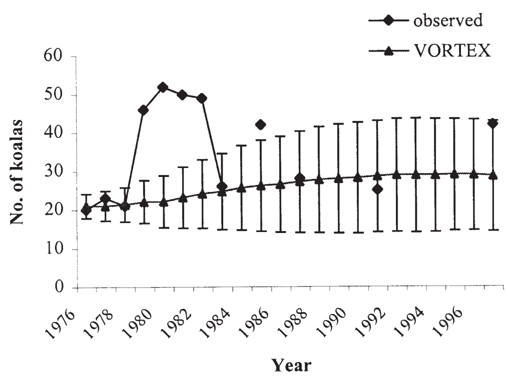

Figure 1. Observed koala population trends and trends predicted by 1000 iterations of VORTEX at (a) Oakey and (b) Springsure (bars show ±1 SD).

nants are as important as the total number of hectares conserved. Hanski (1998) notes that in a metapopulation there are three different forms of habitat loss: removal of patches within one continuous part of the range, random loss throughout the range, and reduction of the area of individual patches. Koalas have experienced each of these processes in parts of their range. Hanski also points out that different forms of habitat loss can result in different predictions for the metapopulation, so modeling of koalas will have to incorporate information on the form of habitat loss.

The other major consideration in modeling is whether to include the demography of other species, such as prey and predators, that interact with the modeled species. Most modeling methods incorporate these factors, usually in a way that does not explicitly model the demography of the other species. Some programs allow the modeler to set trends in the carrying capacity of the habitat or to set a trend in biomass of another species

Table 4. Sensitivity analysis of the effect on probability of extinction (*E*) and growth rate (λ) of varying fertility and mortality relative to standard input (Table 3).

	Oakey		*Springsure*	
Scenario	λ	E	λ	E
Standard	0.930	0.464	1.034	0.084
−10% fertility	0.915	0.608	1.015	0.117
+10% fertility	0.943	0.321	1.052	0.046
−10% newborn mortality	0.936	0.386	1.042	0.053
+10% newborn mortality	0.923	0.504	1.026	0.089
−10% juvenile mortality	0.933	0.418	1.038	0.068
+10% juvenile mortality	0.927	0.488	1.031	0.086
−10% adult mortality	0.936	0.323	1.041	0.042
+10% adult mortality	0.923	0.526	1.028	0.099

with a specified effect on the modeled species. None of these methods allows for complex interactions among species. At Oakey, preliminary data indicate changes in the age structure of the trees in which the koalas live and feed (G.G., A.M.P., and W.B.S., unpublished data). Changes in tree populations could lead to long-term problems for the koalas because their density is influenced by the relative abundance of preferred fodder trees (Melzer 1995).

Recommendations for Modeling in Koala Management

National Koala Conservation Strategy

The primary aim of the National Koala Conservation Strategy is to conserve koalas by retaining viable populations in the wild throughout their natural range (ANZECC 1998). To this end, the strategy puts forward a research agenda aimed at collecting the data necessary for the construction and validation of PVA models in koalas. The recommended research actions include many that could provide data for PVA modeling at a local level: (1) mapping and assessment of koala populations, (2) improving data on koala occurrence and absence now and in the past, (3) collecting reliable historical data on past numbers of koalas and causes of changes in numbers and distribution, (4) identifying and ranking of koala habitat, (5) assessing of koala population dynamics, (6) researching reproductive success and breeding structure in a wide range of koala populations, (7) researching the susceptibility of wild and captive koala populations to disease infection and factors affecting the expression of disease, with particular interest given to chlamydia, (8) establishing rates of increase of selected koala populations to allow prediction of trends in population viability and identification of potential threatening processes, (9) studying movements, home-range sizes, and interactions among threats such as vegetation clearance, vegetation fragmentation, roads, wildfire, and dogs,

(10) researching the effects on koala populations of fire, predators (especially dogs and foxes), motor vehicles, forest fragmentation, and other processes that alter habitat characteristics and processes that magnify these effects, (11) researching genetic variability in existing populations and implications for translocation programs, (12) researching management of overbrowsing by koalas, including approaches to managing habitat and to managing koala populations in overbrowsed habitats, and (13) investigating fertility control of discrete populations.

Forecasting in Local Populations

Action at the local level is vital for conservation, and there is a need to collect appropriate data, predict the outcome of various management scenarios, and decide whether to aid dwindling populations or control booming ones. To this end, the application of PVA forecasting requires a streamlined approach that is robust to deficiencies of data.

A number of koala conferences have identified the role of local government and community groups in koala conservation and the need for researchers and wildlife managers to work with local councils because of their role in determining land use (Lunney et al. 1990; Lunney & Matthews 1997). For example, research in conjunction with shire councils involving community questionnaires and shirewide field surveys (Lunney et al. 1996, 1998, this issue) led to a major development at the state level: the New South Wales State Environmental Planning Policy no. 44 (SEPP 44) on koala habitat protection under the Environmental Planning and Assessment Act 1979. The policy's aim is to protect and restore koala habitat and thus to reverse current koala population decline and ensure a permanent free-living population throughout the species' present range. Local governments are obliged to ensure that developers survey for potential koala habitat when an application affects an area >1 ha in size. If potential habitat is found, a study must be conducted to determine whether core habitat exists. The SEPP 44 defines core koala habitat as an area of land with a resident population of koalas, defined as having breeding females and recent sightings or historical records of a population.

Historical data are important because the amount of unoccupied habitat is critical in metapopulation models (Hanski 1998). Therefore, surveys that rely only on presence and absence of koalas are inadequate for planning, and important habitat must be identified by some other method. If core koala habitat is identified, a plan of management must be prepared before development permits are granted. The planning is not limited to land subject to development: SEPP 44 states that comprehensive plans for koala management may be prepared for an entire local government area, which is the most economical option (Lunney et al. 1999, this issue). Demographic modeling can determine whether the effort made to protect the habitat is likely to be rewarded by a viable population, and the process of testing PVA models in koala populations where extensive data sets are available allows investigation of the minimum data requirements for accurate PVA in koalas.

The koala is often seen as a flagship species whose conservation will aid other species; indeed, even for its own sake, other species cannot be ignored. Therefore, it will be important to model the species with which koalas interact. The koala is an obligate folivore and requires trees for all phases of its activity, including escape from predators, so the demography of the preferred tree species needs to be incorporated into the modeling.

National Forecasting

Assignment of status at the state and national level implies forecasting at that level, but these forecasts are rarely quantitative or explicit. It is principally at the state and national levels that decisions are made about the formal conservation status of koalas, and these decisions affect the level of legal protection and funding. Therefore, it is important that these decisions be based on the best possible information. When applying the concept of triage to koalas, it is important to determine, at the level of the entire species' distribution, what is the likely outcome of continuation of present management and whether a change in management will alter the prognosis for koalas.

Metapopulation modeling requires better estimates of dispersal between pairs of adjacent populations, preferably those that have historical data (Knott et al. 1998), which allows retrospective testing of a metapopulation PVA. For broad application of PVA, simplification of models is important; for example, some metapopulation models incorporate dispersal but ignore details of within-population processes (Hanski 1994; Bradstock et al. 1996). It is also possible to construct a model that assumes complete independence of local populations and uses mean rates and environmental parameters for within-population processes. Given the large errors associated with single-population models, metapopulation models have to be tested carefully before they can be relied upon for either predictions of extinction or assessment of management options. There may be sufficient historical data to test retrospectively whether such models accurately predict regional or national patterns of population extinctions.

Conclusions

Koalas are regarded as near-threatened nationally, varying from secure or overabundant in some areas to vulnerable or extinct in others. Every part of the koala's range has either already experienced change, such as decline, fragmentation, or relocation, or has an uncertain future because of reduced genetic variation. Thus the species is at a point where conservation intervention is needed and could be useful. To adequately manage current threats, we must determine the relative importance of threats in different localities and the likelihood that management of particular threats will alter the koala's prognosis.

The koala's status and appropriate action need to be evaluated at every level from local to national, and the National Koala Conservation Strategy emphasizes the need to obtain information for demographic forecasting. Whether we can make accurate demographic forecasts at the national level is unknown, but if we could, it would enhance our ability to make national management decisions about this species. It is important to investigate the minimum data requirements and the best modeling tools for accurate PVA in koalas. The retrospective tests in Queensland have shown that accurate predictions can be made for local koala populations, which is not only important for koalas but also for general validation of PVA methods. Population viability analysis modeling should take account of koala's interactions with other species, particularly the demography of preferred tree species, which are not necessarily secure.

The genetic structure (management units) of the koala suggest that a metapopulation model would be appropriate when multiple koala populations are modeled. At present, however, there are limited data on dispersal among populations, and no clusters of adjacent populations have been studied to reveal metapopulation processes. Adequate data for a retrospective test of a multipopulation PVA will be far harder to obtain than data for single local populations. There is no need to subdivide a multipopulation PVA into separate analyses for different evolutionarily significant units, because genetic analyses do not reveal any sharp discontinuities in genetic variation. Management plans derived from PVA work, however, should recognize evidence of genetic and morphological differentiation on a north-south axis because it is important to maintain populations throughout the range.

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Literature Cited

Akçakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. Conservation Biology **11:** 422–434.

Australia and New Zealand Environment and Conservation Council (ANZECC). 1998. National koala conservation strategy. Environment Australia, Canberra, Australian Capital Territory.

Bradstock, R., M. Bedward, J. Scott, and D. A. Keith. 1996. Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. Conservation Biology **10:** 776–784.

Brook, B. W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). Biological Conservation **82:**119–128.

Brook, B. W., J. R. Cannon, R. C. Lacy, C. Mirande, and R. Frankham. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). Animal Conservation **2:**23–31.

Ferson, S. 1994. RAMAS/stage: generalized stage-based modeling for population dynamics. Applied Biomathematics, Setauket, New York.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Gordon, G. 1991. Estimation of the age of the koala *Phascolarctos cinereus* (Marsupialia: Phascolarctidae), from tooth wear and growth. Australian Mammalogy **14:**5–12.

Gordon, G., A. S. Brown, and T. Pulsford. 1988. A koala (*Phascolarctos cinereus* Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. Australian Journal of Ecology **13:**451–461.

Gordon, G., D. G. McGreevy, and B. C. Lawrie. 1990*a*. Koala populations in Queensland: major limiting factors. Pages 85–95 in A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. Biology of the koala. Surrey Beatty and Sons, Sydney.

Gordon, G., D. G. McGreevy, and B. C. Lawrie. 1990*b*. Koala population turnover and male social organization. Pages 189–192 in A. K. Lee, K. A. Handasyde, and G.D. Sanson, editors. Biology of the koala. Surrey Beatty and Sons, Sydney.

Haig, S. M., J. R. Belthoff, and D. H. Allen. 1993. Population viability analysis for a small population of Red-cockaded Woodpeckers and an evaluation of enhancement strategies. Conservation Biology **7:**289–301.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology **63:**151–162.

Hanski, I. 1998. Metapopulation dynamics. Nature **396:**41–49.

Houlden, B. A., P. R. England, A. C. Taylor, W. D. Greville, and W. B. Sherwin. 1996. Low genetic variability of the koala (*Phascolarctos cinereus*) in south east Australia following a severe population bottleneck. Molecular Ecology **5:**269–281.

Houlden, B. A., B. H. Costello, D. Sharkey, E. V. Fowler, A. Melzer, W. Ellis, F. Carrick, P. R. Baverstock, and M. S. Elphinstone. 1999. Phylogeographic differentiation in the mitochondrial control region in the koala, *Phascolarctos cinereus* (Goldfuss, 1817). Molecular Ecology **8:**999–1011.

Knott, T., D. Lunney, D. Coburn, and J. Callaghan. 1998. An ecological history of koala habitat in Port Stephens Shire and lower Hunter on the central coast of New South Wales, 1801–1998. Pacific Conservation Biology **4:**354–368.

Lacy, R. C. 1993. VORTEX: a computer simulation for use in population viability analysis. Wildlife Research **20:**45–65.

Lacy, R. C., and T. W. Clark. 1990. Population viability assessment of eastern barred bandicoot. Pages 131–146 in T. W. Clark and J. H. Seebeck, editors. Management and conservation of small populations. Chicago Zoological Society, Brookfield, Illinois.

Lindenmayer, D. B., M. A. Burgman, H. R. Akçakaya, R. C. Lacy, and H. P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife populations. Ecological Modelling **82:**161–174.

Lindenmayer, D. B., R. C. Lacy, and M. L. Pope. 2000. Testing a simulation model for population viability analysis. Ecological Applications:in press.

Lindenmayer, D. B., M. A. McCarthy, and M. L. Pope. 1999. Arboreal marsupial incidence in eucalypt patches in south-eastern Australia: a test of Hanski's incidence function metapopulation model for patch occupancy. Oikos **84:**99–109.

Lunney, D., and A. Matthews. 1997. The changing roles of state and local government in fauna conservation outside nature reserves: a case study of koalas in New South Wales. Pages 97–106 in P. Hale and D. Lamb, editors. Conservation outside nature reserves. Centre for Conservation Biology, University of Queensland, Brisbane.

Lunney, D., C. A. Urquhart, and P. Reed, editors. 1990. Koala summit: managing koalas in NSW. New South Wales National and Wildlife Service, Hurstville.

Lunney, D., C. Moon, and A. Matthews. 1996. A 1990 survey of the koala *Phascolarctos cinereus* population at Iluka in Northern New South Wales. Pages 102–122 in G. Gordon, editor. Koalas: research for management. World Koala Research Incorporated, Brisbane, Queensland.

Lunney, D., S. Phillips, J. Callaghan, and D. Coburn. 1998. Determining the distribution of koala habitat across a shire as a basis for conservation: a case study from Port Stephens, New South Wales. Pacific Conservation Biology **4:**186–196.

Lunney, D., C. Moon, A. Matthews, and J. Turbill. 1999. Coffs Harbour City plan of management. Part A: the plan. New South Wales National Parks and Wildlife Service, Hurstville.

Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a re-evaluation of IUCN threatened species categories. Conservation Biology **5:**148–157.

Maguire, L. A., R. C. Lacy, R. J. Begg, and T. W. Clark. 1990. An analysis of alternative strategies for recovering the Eastern Barred bandicoot. Pages 147–164 in T. W. Clark and J. H. Seebeck, editors. Management and conservation of small populations. Chicago Zoological Society, Brookfield, Illinois.

Mann, C. C., and M. L. Plummer. 1999. A species' fate, by the numbers. Science **284:**36–37.

Martin, R. W. 1981. Age-specific fertility in three populations of the koala, *Phascolarctos cinereus* Goldfuss, in Victoria. Australian Journal of Wildlife Research **8:**275–284.

Martin, R. W. 1985*a*. Overbrowsing and decline of a population of the koala, *Phascolarctos cinereus*, in Victoria. I. Food preference and food tree defoliation. Australian Journal of Wildlife Research **12:** 355–365.

Martin, R. W. 1985*b*. Overbrowsing and decline of a population of the koala, *Phascolarctos cinereus*, in Victoria. III. Population dynamics. Australian Journal of Wildlife Research **12:**377–385.

Martin, R., and K. Handasyde. 1991. Population dynamics of the *koala (Phascolarctus cinereus*) in south-eastern Australia. Pages 75–84 in A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. Biology of the koala. Surrey Beatty and Sons, Sydney.

Martin, R. W., and P. Mitchell. 1988. Population structure and reproductive status of koalas on Rotamah Island. Australian Journal of Wildlife Research **15:**511–514.

Master, L. L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology **5:**559–563.

Maxwell, S., K. Morris, and A. Burbidge, editors. 1996. Action plan for Australian marsupials and monotremes. Environment Australia, Canberra, Australian Capital Territory.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biological Conservation **73:** 93–100.

McCarthy, M. A., D. B. Lindenmayer, and M. Drechsler. 1997. Extinction debts and risks faced by abundant species. Conservation Biology **11:**221–226.

McClanahan, T. R., and R. W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology **7:**279–288.

McIntyre, S., G. W. Barrett, R. L. Kitching, and H. F. Recher. 1992. Species triage: seeing beyond wounded rhinos. Conservation Biology **6:**604.

Melzer, A. 1995. Aspects of the ecology of the koala *Phascolarctos cinereus* (Goldfuss 1817) in subhumid woodlands of central Queensland. Ph.D thesis. University of Queensland, Brisbane.

Mills, L. S., S. G. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology **10:**863–873.

Millsap, B. A., J. A. Gore, D. E. Runde, and S. I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildlife Monographs **111**.

Mitchell, P. J. 1989. The social organization of koalas. Ph.D. thesis. Monash University, Melbourne, Victoria.

Mitchell, P., and R. W. Martin. 1991. The structure and dynamics of koala populations: French Island in perspective. Pages 97–108 in A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. Biology of the koala. Surrey Beatty and Sons, Sydney.

Moritz, C. 1994. Defining "evolutionarily significant units" for conservation. Trends in Ecology and Evolution **9**:373–375.

Possingham, H. P., and I. Davies. 1995. ALEX: population viability analysis model for spatially structured populations. Biological Conservation **73:**143–150.

Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for improved threatened species management using population viability analysis. Pacific Conservation Biology **1:**39–45.

Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology **2:**185–193.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience **1:**131–134.

Sherwin, W. B., and N. D. Murray. 1990. Population and conservation genetics of marsupials. Australian Journal of Zoology **37:**161–180.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371:**65–66.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: Prairie-chickens as an example. Journal of Wildlife Management **61:**302–312.

World Conservation Union. 1994. IUCN red list categories. Gland, Switzerland.