

# The Effect of Road-Based Fatalities on the Viability of a Peri-Urban Swamp Wallaby Population

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## Abstract

Roads and traffic have a multitude of impacts on wildlife populations. Wildlife existing within the confines of fragmented reserves are particularly susceptible to fatalities on roads, especially those situated within urban and semirural matrices. The sustainability of many wildlife populations within reserve fragments are tenuous as roads further subdivide reserved areas and increase the frequency of animal–vehicle contact. Although many studies have assessed the quantity and diversity of fatalities from collisions, few studies have examined the long-term viability of wildlife populations living adjacent to roads. We chose to examine the effects of disturbances, including fatalities on roads, on a population of swamp wallabies (*Wallabia bicolor*) within the Royal National Park on the urban fringe of Sydney, Australia. Despite having an extensive range, researchers suspect that many local populations of this sole member of *Wallabia* are in decline. We used a combination of population modeling and sensitivity analysis to assess the impact of disturbances on the population. Under current conditions, the forecast of the population was to decline over the next 100 years with the possibility of becoming extinct. We found that female reproduction and breeding were most influential on the population model. Of the range of management options investigated, by far the most rewarding was the reduction of fatalities on roads, as only a 20% decrease in female fatalities on roads has the potential to reverse the current decline and represents the best option for maintaining long-term viability. We suggest that documentation and subsequent management of road impacts, within the context of other threats, is essential to the conservation of similar species in road-affected environments. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1615–1624; 2006)

## Key words

Australia, disturbance regimes, metapopulation model, population viability, road-based fatalities, road ecology, Royal National Park, sensitivity analysis, swamp wallaby, *Wallabia bicolor*.

Roads and traffic have well-documented impacts on biota. A growing awareness of the threat of roads on wildlife survival has prompted research that seeks to document impacts and develop mitigation programs (Sherwood et al. 2002, Forman et al. 2003). For wildlife, roads can form barriers to movement leading to fragmentation of populations and isolation from resources and mates (Richardson et al. 1997, Vos and Chardon 1998, Gerlach and Musolf 2000, Dyer et al. 2002, Goosem 2002). Roads also have the potential to alter the structure of populations adjacent to roads where impacts on behavioral patterns and habitat use lead to road avoidance (Forman et al. 2002, Bautista et al. 2004). Perhaps the most important impact though is the wildlife killed through collisions with vehicles. Although numerous studies have described the pattern of wildlife fatalities in different parts of the world (Finder et al. 1999, Hubbard et al. 2000, Joyce and Mahoney 2001, Bautista et al. 2004, Malo et al. 2004, Saeki and Macdonald 2004, Taylor and Goldingay 2004), only a few studies have examined the impact of these fatalities on the persistence of populations (Hels and Buchwald 2001, Lopez 2004). As a source of population mortality, we must consider road-based fatalities along side other human-induced drivers of change like habitat destruction, the introduction of feral predators, and resource competition from introduced animals. As we will show, in some cases fatalities on roads may be the final blow

to native wildlife living in semirural matrices of remnant bushland, agricultural land, and urbanized areas.

That roads may be contributing to population decline is not a new concept. Bank et al. (2002) identified that in areas where diminished natural resources have resulted in rare or endangered species and habitats, roads can have serious impacts on mortality rates of wildlife. The number of animals killed on a road may be low yet still have a devastating effect on the population because of low animal numbers, slow breeding, and interactions with other forms of disturbance (Lunney et al. 2002). The most effective framework for examining the impact of road-based fatalities on wildlife is through metapopulation modeling. The utility of metapopulation modeling through population viability assessment (PVA) is in its ability to assess the impact of the built (in this case the road) and the natural environment on long-term population trends. Population viability assessment is used in conservation biology to assess minimum viable populations (Shaffer 1981, Gilpin and Soule 1986), but it is best utilized when indicating the relative merits of alternative population and habitat management strategies (Boyce 1992, Possingham et al. 1993, Mathews and Macdonald 2001, Lindenmayer et al. 2003). For managers, plausible estimates for the probability of extinction are an integral part of the planning process. In the context of roads, metapopulation models enable researchers to quantify how sensitive wildlife populations are to fatalities on roads and what mitigation targets are required to foster persistence.

By way of an example, we target a population of swamp

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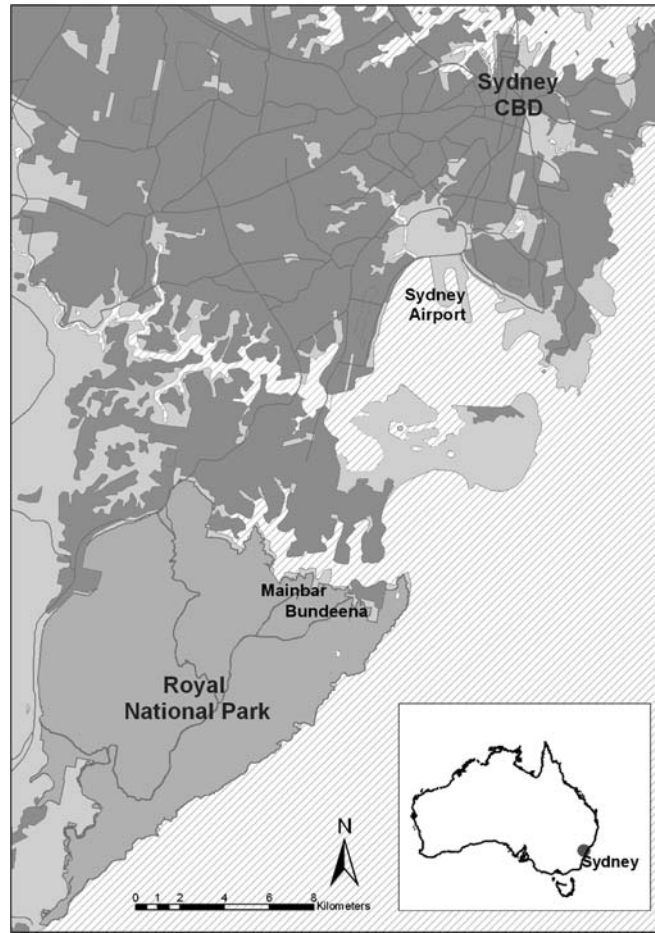
wallabies (*Wallabia bicolor*) within the Royal National Park, Australia. The swamp wallaby is the only member of the monophyletic clade *Wallabia* and has vastly different dentition, genetic, reproductive, and behavioral characteristics from other wallabies (Merchant 2002). While researchers presume the range of the swamp wallaby to be extensive, from Cape York to southern Victoria, we have no information on its abundance within this range. Ben-Ami (2005) reported that despite being typically regarded as resilient to disturbance, the preferred habitat of the swamp wallaby typically coincides with land occupied by humans, placing substantial pressure on local populations. However, Ben-Ami (2005) reported that they are typically cryptic and solitary. Hence, it is of no surprise that they are the last medium-sized marsupial to remain within the boundaries of the Royal National Park. All other large marsupials, such as kangaroos, have already become locally extinct.

In spite of their resilience, Ramp et al. (2006) estimated annual fatalities on roads within the park to be around 130 wallabies, concerning park authorities. Moriarty (2004) estimated that the number of wallabies left within the park was between 400–1,000 individuals, indicating that fatalities are accounting for a substantial proportion of the population each year. Park authorities are also aware of a multitude of other human-induced disturbances, such as habitat loss to suburban and park infrastructure (including roads), competition and predation from nonnative fauna and flora, hunting, human presence, and increasing fire occurrence. In light of this, park authorities have expressed a desire to engage in mitigation measures to reduce the number of fatalities occurring on roads (e.g., through speed reduction). With increasing urban sprawl and a growing trend in using the park as a recreation venue, it is highly likely that traffic volumes will increase in the coming years. Consequently, a robust understanding of how fatalities might be influencing the population as a whole and the setting of mitigation targets to create a viable population are necessary to ensure the survival of this species within the park.

To achieve this goal, our aims were to 1) highlight the impact of roads and other disturbance factors on the swamp wallaby population, 2) identify those factors contributing most to uncertainty in the viability of the population, and 3) to examine the potential benefit of different management options in addressing the causes of decline. In doing so, we sought to highlight the need for conservation planning to accommodate for road impacts, particularly within the urban fringe.

## Study Area

The Royal National Park (34°05'S, 151°05'E) is located within the southern fringe of Sydney, New South Wales, Australia (Fig. 1). As the oldest national park in the world (established in 1879), the geographic proximity of the Royal National Park to Australia's largest city (Sydney, population 4.2 million) presents an interesting conundrum for managers trying to protect the flora and fauna of the park while also providing recreation to 1.25 million visitors per year and



**Figure 1.** The Royal National Park, located on the southern fringe of Sydney, Australia. Light gray = unbuilt areas; medium gray = vegetated areas within the park; dark gray = urban areas; slanted lines = the Pacific Ocean. Medium gray lines represent roads.

residence to over 2,000 people. The park covers 15,068 ha (New South Wales National Parks and Wildlife Service [NSW NPWS] 2000) and has a wide diversity of vegetation communities including heathland, woodland, eucalypt forest, rainforest, wetland, and swamps. The climate is temperate, with average daytime temperatures ranging from 7–17° C in the coolest month of July, to 18–26° C in the warmest month of January. Average annual rainfall is highest in June (126 mm) and lowest in September (62 mm). The park is home to a population of swamp wallabies that is effectively isolated within the park boundaries. On its western and southern limits, the park is bounded by a major highway, partially fenced train tracks, and contiguous urban communities. The Pacific Ocean and a series of bays and inlets mark the eastern and northern boundaries of the park.

The park contains 90 km of single-lane paved roads with various speed zones of 50, 60, and 80 km per hour, although recommended speeds can be as low as 25 km per hour. Traffic volume is comprised mostly of local residents, visitors to the National Park and the township of Bundeena, and NSW NPWS staff. Traffic volume counts collected over 6 months in 2003 recorded the volume of vehicles entering the park at the main entrance on Farnell Avenue at just over

**Table 1.** Current (2005) best estimate values of parameters (plus environmental variation) used in the basic population model for swamp wallabies in the Royal National Park, Australia.

Category	Parameter	Value	Variation	References
Scenario settings	No. of iterations	100		
	No. of yr	100		
	Extinction definition	1 sex remains		
Species description	No. of populations	1		
	Inbreeding depression	None		
	Environmental concordance in survival and reproduction	None		
Reproductive system	Type of mating system	Polygynous		(Ben-Ami 2005)
	Age of first offspring for F	2 yr		(Merchant 2002)
	Age of first offspring for M	2 yr		(Merchant 2002)
	Max. age of reproduction	10 yr		Estimate
	Max. no. of progeny/yr	2		
Reproductive rates	% M at birth	50		(Crebbin 1982, Osawa 1989)
	% ad F in the breeding pool	70	10	Estimate
Mortality rates	Mean no. of offspring/F/yr	1.2	0.3	Estimate
	F mortality from 0–1 yr	25	3	(Ben-Ami 2005)
Catastrophes	F mortality from 1–2 yr	30	3	(Ben-Ami 2005)
	F mortality after 2 yr	20	3	(Ben-Ami 2005)
	M mortality from 0–1 yr	25	3	(Ben-Ami 2005)
	M mortality from 1–2 yr	30	3	(Ben-Ami 2005)
	M mortality after 2 yr	20	3	(Ben-Ami 2005)
	Catastrophe type	Wildfire		
Mate monopolization	Global/local	Global		(NSW NPWS 2000)
	Frequency	0.04		(NSW NPWS 2000)
	Reproduction	0.7		Estimate
Initial population size	Survival	0.9		(Ben-Ami 2005)
	% M in breeding pool	70		Estimate
Carrying capacity	Initial population size	1,000		
	Carrying capacity	1,000		(Robertshaw and Harden 1986, Troy and Coulson 1993, Moriarty 2004, Ben-Ami 2005)
Harvest		None		
Supplementation		None		

<sup>a</sup> NSW NPWS = New South Wales National Parks and Wildlife Service.

1,573 ± 39 (mean ± standard error) vehicles per day (Ramp et al. 2006). Most traffic occurs during the day, however, nighttime vehicles travel faster on average, typically 20 or 25 km per hour above the speed limit.

## Methods

### Population Viability Assessment Model

We constructed a PVA model using Vortex 9.0<sup>®</sup> (Lacy et al. 2005) because it is robust to the documented uncertainties inherent in PVA when making population predictions (Lindenmayer et al. 1995). To model the swamp wallaby population in the Royal National Park, our approach consisted of 1) a best-estimates basic model, 2) sensitivity testing of the model to sensitive parameters, and 3) the prioritizing of theoretical management actions that target those sensitive parameters most influencing the population model. We described (Table 1) and justified parameter estimates used in the following sections.

### Reproductive System

Merchant (2002) reported that maturity in swamp wallabies often occurs between 15 and 18 months. For modeling purposes, we set adulthood at 2 years because Vortex can only handle integer values for adulthood and this is more

realistic than allowing for adulthood at age 1 year. We included 2 other age classes: pouch young aged less than 1 year and juveniles aged between 1 and 2 years. Information on the breeding pool in swamp wallaby populations is sparse. Under high predation pressure, populations switch from seasonal to continuous breeding cycles (Robertshaw and Harden 1986), yet this situation is unlikely in the Royal National Park. Documented estimates of pregnancy rates of 75.3% and females with pouch young of 86.5% in southeastern Victoria suggest that the percentage of females in the breeding pool may lie around 80%. To be conservative, we chose a value of 70% but included a large degree of variation about this value (20%) to explore the effect of female breeding over a range of plausible values, ranging from 50% to 90%. To account for the influence of red fox (*Vulpes vulpes*) predation on breeding, we chose to increase the percentage of females in the breeding pool marginally in relation to the sequential removal of foxes. There is currently no published information on how predation affects breeding success, but it is highly likely that an effect exists.

Merchant (2002) reported that potential breeding frequency of females was one offspring every 8 months. In addition, one captive study has observed a lack of hierarchy

in access to females by males (Crebbin 1982). Despite being solitary, we know that swamp wallabies typically occur at higher densities within gullies, enabling contact with numerous potential mates (Ben-Ami 2005). Given this knowledge, a breeding rate of 1.5 offspring per year would be the upper limit of breeding capability. We therefore set the mean offspring rate per female per year at 1.2 with a standard of deviation of 0.3 to reflect this upper limit, as well as allowing for leaner years where the mean offspring rate per female per year was only 0.9.

### Mortality Rates

Mortality rates for the population of swamp wallabies within the Royal National Park are mostly unknown, yet we were able to assume plausible bounds for rates based on information from similar populations and expert knowledge. In the nearby Muogamarra Nature Reserve, Ben-Ami (2005) estimated that natural causes of mortality due to disease and old age affect 10% of the swamp wallaby population. We therefore used a similar rate. In contrast, we were able to obtain local information on fatalities on roads from a 6-month study of swamp wallaby fatalities over 22 km of road in 2003 that estimated 0.04 fatalities per kilometer per day (Ramp et al. 2006). We extrapolated this figure over the 90 km of paved roads within and bordering the Royal National Park to arrive at a figure of 130 swamp wallaby fatalities per year, equating to approximately 10% of the initial population estimate. Our estimate is conservative, however, as it is common for fatalities to go unrecorded when animals are not initially killed outright and have the opportunity to leave the roadside or are scavenged by predators (Slater 2002). Fatalities are typically biased towards subadults, so we set fatalities of subadults at 15% (Coulson 1982, Osawa 1989, Jones 2000, Klöcker 2003).

Paplinska et al. (2003) reported that in a population of swamp wallabies in southeastern Victoria, male bias was 1.84:1; however, these data were obtained from culled animals and this process may favor males as females have been observed to use landscape inaccessible to shooters, such as the bottom of gullies (Ben-Ami 2005). Given a lack of specific information for the Royal National Park, we did not use a sex bias in mortality, assuming equal dispersal of both male and female wallabies. The threat of predation by red foxes is likely to affect pouch young and juveniles rather than adults as foxes typically prefer dietary items weighing between 35 and 5,000 g (Burbidge and McKenzie 1989). Swamp wallabies are not, however, the preferred prey of foxes, as they have been observed to typically comprise only a small proportion of their diet (Augee et al. 1996, Meek and Triggs 1998). We estimated mortality to predation at 5% per annum for both juvenile classes in line with the known increase in mortality of these age classes (Higginbottom 2000, Banks 2004), as no accurate information on loss to predation is currently available for our region. Given the above estimates of mortality, we attributed noncatastrophe annual mortality in the Royal National Park to natural mortality, predation, or road-based fatalities as detailed in Table 2.

**Table 2.** Estimates of current (2005) percentage of annual female mortality (FM) for swamp wallabies of different age groups within the Royal National Park, Australia.

Mortality source	FM: 0–1 yr	FM: 1–2 yr	FM: >2 yr
Natural mortality	10	10	10
Predation	5	5	0
Road fatalities	10	15	10
Total mortality	25	30	20

### Catastrophes

Wildfires are the most probable cause of catastrophes within the Royal National Park. The 2 most recent large-scale wildfires occurred in the park in 1988 and in 1994. Consequently, we set the probability of a catastrophic event occurring at 0.04 per year (NSW NPWS 2000, Ben-Ami 2005), although we also considered the occurrence of wildfires at frequencies of 0.03 and 0.06 given the lack of historical data and the documented variation in catastrophic events.

We found relatively little information on the survival and reproduction of swamp wallabies after fire and certainly no published information. Unpublished research suggests that the survival of swamp wallabies can be high if the area burnt by wildfire has previously had some form of fire-severity management to reduce the fire intensity (N. Garvey, University of New South Wales, unpublished data), although survivorship can decline in unmanaged areas. Indeed, swamp wallabies have been shown to thrive in burnt habitat (Lunney and O'Connell 1988). We therefore assumed that, given the fire history of the Royal National Park and the moderate size of the swamp wallaby population, it is unlikely that wildfire would dramatically influence numbers of individuals. Accordingly, we set survival at 0.9 but with a range of 0.5 to 0.9 in the sensitivity analysis to account for the patchy nature of fire severity and intensity. Given the likelihood of high survivorship after fire, we chose to not to alter the proportion of females breeding in the population.

### Initial Population Size

Moriarty (2004) conducted population assessments using fecal pellet counts and known defecation rates to estimate the population in the Royal National Park to be 402 in 1999, 328 in 2000, and 381 in 2001. However, pellet-based population surveys tend to be inaccurate as pellet degradation can lead to an underestimation of population size (Johnson and Jarman 1987). Consequently, we decided to set the initial population size at an optimistic 1,000 individuals.

### Carrying Capacity

Population surveys from other locations suggest wallaby density estimates can range from 17/km<sup>2</sup> (Robertshaw and Harden 1986) to 32/km<sup>2</sup> (Troy and Coulson 1993). Based on these values and an area of 150 km<sup>2</sup>, we estimated that the carrying capacity could range from 2,550–4,800 individuals. Swamp wallabies are solitary in nature (Ben-

**Table 3.** Estimates of current (2005) parameter ranges used in the sensitivity analysis for swamp wallabies in the Royal National Park, Australia.<sup>a</sup>

Category	Parameter	Plausible range of values
Reproductive rates	Ad F in the breeding pool	50, 60, 70, 80, 90
Mortality rates	F mortality: 0–1 yr	15, 20, 25, 30, 35
	F mortality: 1–2 yr	20, 25, 30, 35, 40
	F mortality: >2 yr	10, 15, 20, 25, 30
	M mortality: 0–1 yr	15, 20, 25, 30, 35
	M mortality: 1–2 yr	20, 25, 30, 35, 40
Catastrophes	M mortality: >2 yr	10, 15, 20, 25, 30
	Frequency	3, 4, 5, 6
	Reproduction <sup>b</sup>	0.5, 0.6, 0.7, 0.8, 0.9
	Survival <sup>c</sup>	0.6, 0.7, 0.8, 0.9
Initial population size		600, 1,000, 1,400, 1,600
Carrying capacity		1,000, 2,000, 3,000, 4,000, 5,000

<sup>a</sup> All values are percentages except for reproduction and survival, which are probabilities.

<sup>b</sup> Proportion of wallabies reproducing.

<sup>c</sup> Proportion of wallabies surviving.

Ami 2005), and although their home ranges do overlap, individuals tend to differ in their temporal usage of space. Consequently, the carrying capacity of the swamp wallaby population in the Royal National Park is limited by the availability of space as well as other resources such as access to food and water (Ben-Ami 2005). In addition, the introduced rusa deer (*Cervus timorensis*) competes for resources and is thought to be limiting recruitment in the swamp wallaby population (Moriarty 2004). Accordingly, we chose to examine a range of carrying capacities from 1,000 to 5,000 individuals.

### Sensitivity Analysis

To assess predictions over a range of plausible parameter values, we implemented sensitivity analyses following the specifications described by McCarthy et al. (1996). We considered a parameter for sensitivity analysis if there was uncertainty in its estimation or if we suspected it might influence the population model (Table 3). We selected parameters associated with fecundity, mortality, catastrophic events, and initial population size. We chose the range of variation of each parameter to reflect both the scale of uncertainty in its estimation and knowledge of the biology of the swamp wallaby (McCarthy et al. 1996). We simulated the model 100 times for combinations of the best- and worst-case values to obtain more precise predictions of population viability under extreme circumstances (McCarthy et al. 1996).

We used a random sampling program (Ben-Ami 2003) to generate 500 random combinations of the sensitive parameters over their possible ranges. We ran a PVA model for each combination while we held all other parameters constant. We derived the mean probability of extinction from 100 models, each run over 100 years (50,000 permutations; McCarthy et al. 1996).

We used linear regression to examine the influence of sensitive parameters on the probability of extinction. We examined the contribution of the parameters to the total explained variation by the model using hierarchical partitioning (Mac Nally 2000, 2002, Quinn and Keough 2002), with  $R^2$  used to underlie the partitioning of variation for the

entire hierarchy of models. We ran the model in the R statistical package v2.0.1 (R Development Core Team 2005). We then re-ran best-estimate models with small fluctuations in parameters contributing most to the regression model. We examined forecasted populations after 100 years and 100 simulations to assess the effect of these parameters on long-term population viability.

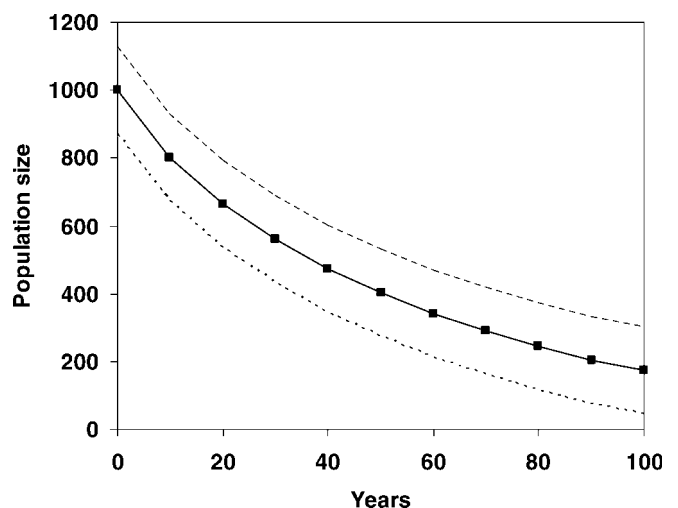
## Results

### The Basic Model

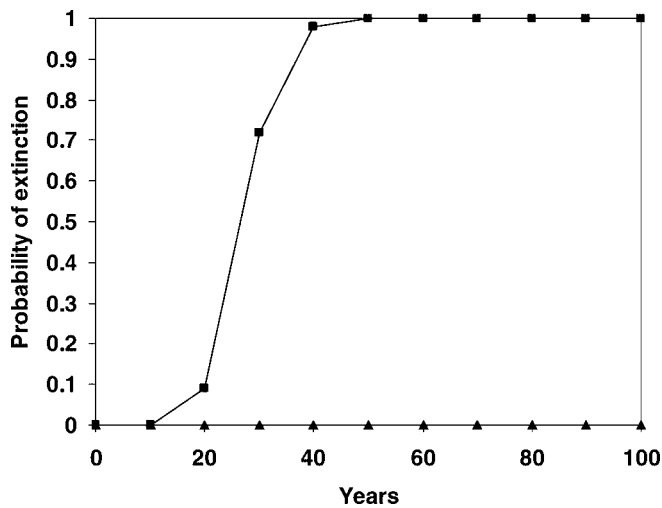
The basic PVA model indicated a drop in population from the initial size of 1,000 individuals to  $100 \pm 129$  (mean of successful populations  $\pm$  SD) over 100 years, declining at a rate of  $-0.017$  individuals per year. The uncertainty about the mean indicates that the population runs a risk of local extinction within the next 100 years (Fig. 2).

### Sensitivity Analysis

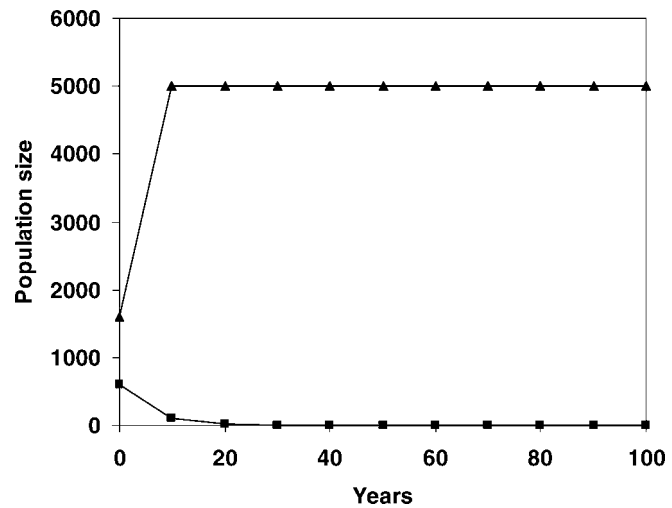
There was a dramatic difference in the probability of extinction within 100 years between the best- and worst-case scenarios of sensitive parameters (Fig. 3). When we



**Figure 2.** Best estimate for the mean swamp wallaby population in the Royal National Park, Australia (2005–2105). The stippled line indicates upper and lower limits of the standard deviation.



**Figure 3.** Mean risk of extinction forecasts over 100 years using the best- and worst-case scenarios for the swamp wallaby population in Royal National Park, Australia (2005–2105). Triangles and squares indicate the forecasts of the best-case and worst-case parameter values, respectively.



**Figure 4.** Mean population forecasts over 100 years using the best- and worst-case scenarios for the swamp wallaby population in Royal National Park, Australia (2005–2105). Triangles and squares indicate the forecasts of the best-case and worst-case parameter values, respectively.

used optimistic conditions, there was a 0% predicted risk of extinction and the population remained at carrying capacity. In contrast, when we used pessimistic conditions there was a 100% risk of extinction, with the population declining rapidly ( $-0.246$  wallabies/yr, reaching extinction within 25 yr, Fig. 4). Of the 12 sensitive parameters we identified in the regression, the increase in survival of catastrophes and the percentage of adult females in the breeding pool significantly reduced the probability of extinction ( $P < 0.001$ ; Table 4). Female mortality of all 3 age classes also contributed significantly to the probability of extinction ( $P < 0.001$ ). We found that the independent contribution to the total explained variation in extinction probability was highest in the mortality of females older than 2 years and in the percentage of adult females in the breeding pool. For the 4 most sensitive parameters, variation of  $\pm 10\%$  about their best estimate values was enough to result in either positive or negative population growth rates (Table 5). As such, we project that management actions designed to target those parameters, however slightly, should have considerable impact on the population model.

### Management Scenarios

We explored a range of management scenarios to examine their effect on the population. The high survival rate associated with wildfires and the negligible impact of increased carrying capacity on the model suggest that wildfire and deer management would not be effective management actions on their own to prevent the decline in the swamp wallaby population (Table 4). Accordingly, we further explored only incremental decreases of 20% in mortality from predation and road-kill. We found that reducing fatalities of females (regardless of age class) by only 20% on roads had a dramatic impact on the viability of the population, and any reduction greater than this resulted in the population reaching carrying capacity (Table 6).

Managing the red fox population also had a beneficial impact on the swamp wallaby population, but this effect was not as dramatic as reducing fatalities on roads (Table 7). The growth rate of the swamp wallaby population switched from negative to positive only after the prevention of 60–80% of fox-related fatalities. When we reduced fox-related fatalities by 80%, the population remained at carrying capacity throughout the 100-year cycle of the model. Road management, as a means of reducing fatalities and increasing reproduction, is clearly the most beneficial approach to reversing the current trend of population decline.

### Discussion

The swamp wallaby is currently thought of as an example of a medium-large species that is suited to surviving within urbanized environments (Ben-Ami 2005). Indeed, other than the eastern grey kangaroo (*Macropus giganteus*), it is one of the last of the macropodids to remain in human-disturbed landscapes in Australia. Despite this resilience, we have shown that pressure on local populations from fatalities caused by collisions with vehicles on roads is a serious issue for local population viability. By way of an example, we predicted that under current conditions within the Royal National Park, the swamp wallaby population would decline steadily over the next 100 years. Driving this process were female mortality and breeding success—the keys to understanding how best to prevent this decline. However, confidence about the estimated values of these parameters requires improving, as researchers have not conducted any intensive surveys to assess them. We suggest that researchers should target these variables to gain a better understanding of their impact on the survival of this species.

Knowledge of how these processes affect population viability enabled us to explore the efficacy of a variety of management strategies that park authorities could adopt. Our PVA analyses indicated that we could reverse the

**Table 4.** The contribution of sensitive parameters to the population decline of swamp wallabies in the Royal National Park, Australia, predicted between 2005 and 2105.<sup>a,b</sup>

Parameter	Estimate	SE	t-value	P	Contribution
(Intercept)	0.284	0.170	1.674	0.095	
Ad F in the breeding pool	-0.018	<0.001	-21.529	<0.001	28.14
F mortality: 0-1 yr	0.016	0.002	9.553	<0.001	5.53
F mortality: 1-2 yr	0.016	0.002	9.856	<0.001	6.76
F mortality: >2 yr	0.044	0.002	26.362	<0.001	44.19
M mortality: 0-1 yr	0.002	0.002	1.180	0.239	1.98
M mortality: 1-2 yr	-0.001	0.002	-0.311	0.756	1.36
M mortality: >2 yr	-0.001	0.002	-0.56	0.576	1.31
Catastrophe frequency	0.014	0.011	1.308	0.192	1.54
Postcatastrophe reproduction	-0.051	0.083	-0.609	0.543	1.37
Postcatastrophe survival	-0.512	0.108	-4.764	<0.001	4.11
Initial population size	-0.001	<0.001	-1.887	0.060	2.09
Carrying capacity	-0.001	<0.001	-0.812	0.417	1.61

<sup>a</sup> We present regression coefficients, significance, and the independent contribution (%) of each parameter to the total explained variation in the response, determined by hierarchical partitioning.

<sup>b</sup> (+) contributes to decline; (-) contributes to growth.

decline in the population by reducing the number of female wallabies killed on roads or reducing predation by red foxes. The major benefit of our approach is that we have been able to establish targets for each management option. For red fox management, an 80% reduction of mortality was necessary to reverse the decline, whereas a reduction of only 20% of female swamp wallaby fatalities on roads was necessary to bring the population close to carrying capacity. This suggests that although red fox reduction is an important management tool and has many potential benefits, it would appear that the target of reducing fatalities on roads is more achievable in the short term. However, the observed trends rely upon the assumption that red fox predation only marginally increases the reproductive output of wallabies (with the percentage of females in the breeding pool used as a surrogate for this, Table 7). However, we know that any increase in breeding females can have a dramatic impact on viability (Table 5). Without any documented evidence of the potential for reproduction to increase after red fox reduction, it remains plausible that this strategy could be a very effective management tool. In addition to road fatalities and predation, fire regimes and competition from rusa deer are also important factors limiting the swamp wallaby population, but our metapopulation model suggest that manage-

ment of these factors will only marginally improve the long-term viability of the population.

Although we could not verify model forecasts for this study (as is typically the case in PVA studies), the swamp wallaby population within the Royal National Park can be confidently modeled (Lindenmayer et al. 2003) as it is a single population enclosed by natural and human-made boundaries. In addition, habitat and climatic conditions are mostly uniform throughout the park. To model the swamp wallaby population, we have drawn upon information of life history parameters known by park managers and other researchers working within the Royal National Park, information described for the nearby Muogamarra Nature Reserve (Ben-Ami 2005), and information from other studies that have accumulated knowledge on habitat use, social structure, anthropogenic disturbances, reproduction, and dispersion dynamics (Edwards and Ealey 1975, Robertshaw and Harden 1986, Osawa 1989, Troy and Coulson 1993, Moriarty 2004). Despite this information, our population modeling has highlighted a number of areas where specific information on life history parameters needs further quantification to improve future modeling.

While metapopulation modeling can evaluate the impact of fatalities on population viability and enable the prescribing of management targets (e.g., a reduction of 20% female

**Table 5.** The influence of the most sensitive parameters on the population model for swamp wallabies in the Royal National Park, Australia, predicted between 2005 and 2105.<sup>a</sup>

Parameter	BE	SA	N <sub>100</sub>		R	
			Mean	SD	Mean	SD
F mortality: 0-1 yr	25	15	842	171	0.011	0.009
			17	12	-0.056	0.123
F mortality: 1-2 yr	30	20	870	151	0.010	0.066
			18	14	-0.055	0.126
F mortality: >2 yr	20	10	985	40	0.051	0.067
			0	0	-0.097	0.146
Ad F in the breeding pool	70	60	16	11	-0.057	0.128
			853	168	0.011	0.068

<sup>a</sup> BE (%), best estimates; SA (%), values used in the sensitivity analysis; N<sub>100</sub>, mean population after 100 years; R, population growth rate.

**Table 6.** The influence of fatality reduction on roads on the population model for swamp wallabies in the Royal National Park, Australia, between 2005 and 2105.<sup>a</sup>

Fatality reduction <sup>b</sup>	F mortality			N <sub>20</sub>		N <sub>50</sub>		N <sub>100</sub>		R
	0–1 yr	1–2 yr	>2 yr	Mean	SD	Mean	SD	Mean	SD	
20	8	12	8	896	121	866	143	876	143	0.010
40	6	9	6	978	46	982	43	973	49	0.038
60	4	6	4	988	39	991	23	989	24	0.065
80	2	3	2	994	22	996	21	995	23	0.091
100	0	0	0	997	12	997	20	994	29	0.118

<sup>a</sup> Female mortality is the percentage of female fatalities on roads for each age group. N<sub>20</sub>, N<sub>50</sub>, and N<sub>100</sub> is the mean population after 20, 50, and 100 years, respectively. R is the population growth rate.

<sup>b</sup> The percentage of the female population lost to fatalities on roads was successively reduced in 20% increments.

mortality on roads), it cannot define the best way to achieve this without the testing of management techniques. The efficacy of various mitigation measures for reducing the impacts of roads have been the subject of much research both overseas (Waring et al. 1991, Groot Bruinderink and Hazebroek 1996, Romin and Bissonette 1996, Clevenger et al. 2001) and in Australia (Mansergh and Scotts 1989, Jones 2000, Bender 2001, Abson and Lawrence 2003). Managers need to customize mitigation strategies to the species in question and implement them at known problem sections of road (Ramp et al. 2005). While many large placental mammals are migratory and often cross roads during their migration, Australia's marsupial mammals typically have fixed home ranges and therefore engage with the road environment in different ways. For the swamp wallaby in the Royal National Park, reduced speed limits at known fatality hotspots along with strategies to improve education and awareness of park users would help to achieve the necessary reduction in fatalities. Additional strategies such as fences and underpasses could also be trialed. This species is not rare or threatened within its range and does not normally warrant conservation action. However, the predicted decline in population suggests that management of the impacts of roads is necessary if park authorities are to maintain the long-term viability of this species.

## Management Implications

There is little doubt that road-based fatalities directly cause local population decline for many species. Fatalities on roads are arguably one of the more predictable, and therefore manageable, types of disturbances facing wildlife popula-

tions in fragmented reserves. Other types of disturbances such as human presence, predation, and interspecific competition have spatially unpredictable impacts, whereas wildfires are neither predictable in space nor time. Vehicles that collide with wildlife and cause fatalities (and road aversion) travel on known routes and therefore have highly predictable dispersion patterns. From a management perspective, this means that the disturbance caused by vehicles are easily targeted, although methods for successfully reducing fatalities are sometimes unpopular and ineffective (Forman et al. 2003). With the aid of metapopulation modeling techniques, we suggest that road management has the potential to be a cost-effective investment and long-term solution to achieving sustainable wildlife populations in highly disturbed environments.

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**Table 7.** The influence of fox reduction on the population model for swamp wallabies in the Royal National Park, Australia, between 2005 and 2105.<sup>a</sup>

Fox reduction <sup>b</sup>	F mortality			N <sub>20</sub>		N <sub>50</sub>		N <sub>100</sub>		R
	0–1 yr	1–2 yr	FR	Mean	SD	Mean	SD	Mean	SD	
20	4	4	71	758	163	544	206	385	209	-0.010
40	3	3	72	840	133	745	199	642	219	0.000
60	2	2	73	876	114	846	150	831	187	0.009
80	1	1	74	940	76	938	79	924	103	0.017
100	0	0	75	961	72	953	69	960	66	0.026

<sup>a</sup> Female mortality is the percentage of females killed by predation for each age group. FR is percentage of reproducing females in the population. N<sub>20</sub>, N<sub>50</sub>, and N<sub>100</sub> is the mean population after 20, 50, and 100 years, respectively. R is the population growth rate.

<sup>b</sup> Mortality due to foxes was successively reduced in 20% increments.

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