POPULATION DYNAMICS AND SURVIVAL OF AN ENDANGERED WALLABY: A COMPARISON OF FOUR METHODS

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Abstract. The bridled nailtail wallaby *Onychogalea fraenata* is a critically endangered marsupial, now restricted to a single locality in central Queensland, eastern Australia. Its small size and its nocturnal, solitary, and cryptic behavior present problems for monitoring of population dynamics. The population apparently declined during a major drought between 1991 and 1995, when juvenile survival was low. We carried out a detailed demographic analysis from 1994 to 1997 in order to estimate survival and abundance in two different habitats, using mark–recapture, mark–resight, radio-tagging, and line-transect methods. The finite rate of increase (λ) and its sensitivity to changes in survival and reproduction of each age class were also calculated using a matrix population projection model. We then assessed biases and the value of each method for management. For data other than those based on radio-tagging data, population size and survival estimates were negatively biased and had large confidence limits. Line-transect estimates were likely to be the least biased. The reasons were that probabilities of capture and sighting varied among sexes, sites, and times; habitat use varied according to vegetation conditions; and the populations were small. Despite this, all methods indicated an increasing population size. The projected value of λ based on radio-tagging data was most sensitive to adult survival. Vegetation conditions improved throughout the study after an initial drought, and the mean projected intrinsic rate of increase was 28% per year. We conclude that management should aim to increase adult survival via predator control and that line-transect estimation is the most appropriate long-term monitoring method.

Key words: *age-specific survival; bridled nailtail wallaby; conservation; demography; elasticity; life history; line transect; Macropodidae; mark–recapture; matrix model;* Onychogalea fraenata; *population dynamics.*

INTRODUCTION

Demographic information is critical for making informed management decisions, particularly for small populations (Caughley and Gunn 1996). It is notoriously difficult to detect changes in small populations by estimating abundance, however, and a more informative approach may be to model population dynamics using data on age-specific survival and fecundity (Taylor and Gerrodette 1993). Sensitivity analysis provides a way to identify vulnerable stages in the life cycles of endangered species (Heppell et al. 1994, Marshall and Crowder 1996, Silvertown et al. 1996, Wisdom and Mills 1997). Stage-classified matrix models are used to calculate age-based measures of life history traits such as the life-span and net reproductive rate, as well as the finite rate of increase (Cochran and Ellner 1992). The elasticities of elements in the resulting matrix population model indicate which vital rate has the greatest proportional effect on the finite rate of increase, λ (DeKroon et al. 1986, Caswell 1989). Ac-

curate estimates of age-specific survival and reproductive rates are needed to parameterize matrix models. There have been many recent improvements in maximum likelihood methods to estimate survival and abundance of animals from mark–recapture, radio-tagging, and distance data from line-transect counts (Lebreton et al. 1992, Buckland et al. 1993, White 1993). For all of these methods, it is crucial to identify and account for departures from the models' assumptions to interpret the results (Burnham et al. 1987, Burnham and Anderson 1992).

The bridled nailtail wallaby *Onychogalea fraenata* is a continuously breeding, medium-sized marsupial (3–8 kg). It suffered a severe range and population decline in the early 20th century and was presumed to be extinct until rediscovered in 1973 (Gordon and Lawrie 1980). The decline was probably due to a combination of large-scale clearing, grazing, and droughts that removed understory shelter and food, and predation by predators (Maxwell et al. 1996). The only remaining wild population survives on a conservation reserve, Taunton National Park (Scientific), in central Queensland. Wallabies are patchily distributed within the 11 000-ha reserve, and are most common at two sites covering ~700 ha. The reserve is affected by

droughts every ~10 years, on average (Evans 1992), and this study commenced at the beginning of the final year of a severe 4-yr drought. Bridled nailtail wallabies are nocturnal and solitary (Fisher 1999*b*). They prefer forest edges and shelter in dense cover (Evans 1996). Adults are preyed on by dingoes, which are common. Around one-half of all deaths of radio-collared adults between 1994 and 1997 were due to dingoes (Fisher 1999*a*). The main cause of mortality in juveniles (i.e., young that have left the pouch but are not yet weaned) is predation by feral cats, and juvenile survival was lower during the drought than afterwards (Evans 1992, Fisher 1999*a*).

The goals of this study were (1) to obtain population size and survival estimates using mark–recapture, mark–resight, radio-tagging, and line-transect methods; (2) to assess the value of these methods for management; (3) to obtain estimates of vital rates, particularly for longevity and the intrinsic rate of increase; and (4) to determine which life history stages have the greatest effect on the rate of population increase.

We first model the relationships of sex, site, year, rainfall, and dingo activity with survival of adults. Departures from the model's assumptions are assessed, and the best estimates of survival are used to construct a matrix population model. We then determine the sensitivity of the population growth rate, λ to changes in survival during early pouch life, late pouch life, juvenile, and adult stages, and to changes in fertility.

METHODS

Study sites

The two sites had different disturbance histories, vegetation types, and histories of occupancy by bridled nailtail wallabies. Food availability was similar, but shelter availability differed between them (Fisher 1999*a*). Taunton National Park (23°33′ S, 149°13′ E) consists of two former cattle properties. Site one (~450 ha) was already cleared when the first property was purchased in 1979, but brigalow (*Acacia harpophylla*) and yellowwood (*Terminalia oblongata*) trees have now regrown from root stock to form a dense forest ~4 m tall. Clearings were created along some tracks by managers in 1994, and the site is adjacent to two cleared paddocks. A second property was added to the park in 1986. Site two (~150 ha) on this property consisted of a mosaic of open riverine swamp with leichardt bean (*Cassia brewsteri*), part of which forms a central cleared paddock, surrounded by ridges with rosewood forest (*Acacia rhodoxylon*) and open poplar box (*Eucalyptus populnea*) woodland. Wallabies have apparently been present in this area since gazettal, but have only been common at site one since about 1990. Park managers bait dingoes with 1080 (sodium monofluoroacetate)-poisoned meat in winter of most years, and carry out quarterly 4-d long surveys over the whole park to monitor wallaby abundance (Lundie-Jenkins et al. 1998).

Trapping and handling

We trapped wallabies in 16 wire cage traps (380 × 380 × 760 mm, Mascot traps, Sydney, Australia) placed at intervals of ~200 m throughout the sites during 13 quarterly field trips between November 1993 and December 1996. Field trips lasted 4–5 wk, and each began with 1 wk of trapping at each site consecutively. Traps were set at pasture edges 1 h before dusk, checked every 3–4 h, and closed between 0230 and 0500 hours. Wallabies were marked using two identical ear tags that had reflective plastic welded to them on both sides in a unique combination of colors. In total, 125 adults were captured at site one, and 28 at site two. The sex ratio of adults captured was 0.8 male : 1.0 female.

Radiotelemetry, line-transect counts, and resighting

Adult wallabies, 32 at site one and 22 at site two, were fitted with radio collars weighing ~30 g and having battery lives of ~20 mo (Sirtrack, Havelock North, New Zealand). Transmitters had mortality-sensing switches, which indicated whether they had remained still for >30 h. Nine juveniles at site one and six at site two were also fitted with 5-g radio transmitters on expandable collars with foam inserts, with battery lives of 6–10 mo (Holohil, Carp, Canada, or Sirtrack). During field trips, radio-tagged wallabies were checked at least twice a week. We estimated the week of death of wallabies that died between field trips from the state of the carcass.

Line-transect counts were carried out at site one by spotlighting between 2000 and 2300 hours at 10 km/h from a vehicle along dirt tracks, on the 10 nights following the week of trapping. We used six transects on an 18-km set route that ran along the four sides of the site, and diagonally across in two directions. This route included all available tracks. The same observer (D. O. Fisher) recorded sightings of all marked and unmarked wallabies and dingoes with a microcassette recorder. We identified tagged wallabies individually, and recorded the distance and angle between the edge of the track and each wallaby seen, with respect to landmarks and numbered posts placed at 25-m intervals along tracks.

Population size and density

Population size was calculated using three methods. Firstly, closed population estimates were obtained from capture records within field trips using CAPTURE (Otis et al. 1978, White et al. 1982). The analysis procedure incorporates the effect on population estimates of unequal capture probability due to individual variation, variation over time, or behavioral responses to trapping (White 1993, Koper and Brooks 1997). Secondly, we used the number of radio-tagged wallabies

and the total number seen during transect counts at site one to calculate Lincoln-Petersen population estimates for each day, and combined the daily estimates for each field trip using the joint hypogeometric maximum likelihood estimator (JHE) with NOREMARK (Bartmann et al. 1987, Neal et al. 1993, White 1993).

Thirdly, we used DISTANCE to calculate densities at site one from line-transect data pooled over each field trip (Buckland et al. 1993), and multiplied these values by the area of the site. Distances between the edge of the road and individual wallabies were initially recorded in 5-m categories, but were pooled into 10-m blocks if visual inspection of the data suggested reactive movement away from the line, and 5% of the tail of the detection histogram was truncated to facilitate modeling (Buckland et al. 1993). The power of this sampling regime was assessed with the power analysis method of Gerrodette (Gerrodette 1987), using the program TRENDS (Gerrodette 1993). The mean intrinsic rate of increase was calculated from all three types of population size estimates by fitting a regression line through the natural logarithms of the data points vs. the time in years, as in Caughley and Sinclair (1994).

Survival

We estimated survival rates of marked wallabies and tested hypotheses using capture–recapture maximum likelihood estimation techniques (Lebreton et al. 1992, 1993). We used MARK (White and Burnham 1997) to fit Cormack-Jolly-Seber (CJS) models to the capture and the resighting data separately for adults. We first investigated the degree to which our data conformed with model assumptions by conducting goodness-of-fit tests (Burnham et al. 1987). The effects of sex, site, rainfall, food biomass (Fisher 1999a), dingo activity, and time (trip, season, and year) on survival and capture probabilities were then assessed. Model selection was based on the corrected Akaike Information Criterion (AICc), a second-order adjustment to the AIC to adjust for bias due to small sample size (Hurvich and Tsai 1989, Anderson and Burnham 1994, Buckland et al. 1997). Akaike weights were used to assess the relative probability of each model being correct (Anderson and Burnham 1994, Buckland et al. 1997). We followed the procedure recommended by Anderson and Burnham (1994) and White and Burnham (1997) in choosing the model with the lowest AICc. We also tested the specific hypotheses of time, sex, site, dingo abundance, food biomass, and rainfall dependence on survival and capture probabilities, using likelihood ratio tests.

We tested for survival rate differences between age classes, sexes, years of tagging, and sites in the 55 adult and 15 juvenile radio-tagged wallabies from both sites combined, using Cox's Proportional Hazards Regression (Cox 1972, Pollock et al. 1989), with the PHREG procedure of SAS (SAS Institute 1989). This method
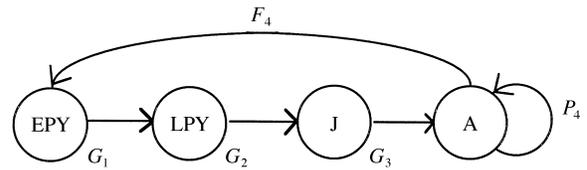

FIG. 1. The life cycle of the bridled nailtail wallaby. EPY, early pouch young (0–2 mo); LPY, late pouch young (2–4 mo); J, juveniles (4–6 mo); and A, adults (>6 mo). G represents the probability of surviving and growing to the next size class at the next time interval, P represents the probability of surviving to remain in a class at the next time interval, and F represents the fertility of the stage that gives rise to stage 1 (EPY) young. Arrows indicate transitions that are possible.

allows for both staggered entry and right censoring due to radio failure and survival past the end of the study.

Population modeling

We identified four life history stages for the transition matrix model: early pouch young (EPY), late pouch young (LPY), juveniles (J), and adults (A). The population was modeled assuming a birth-flow process. A partial life history graph was constructed that which represents all allowable transitions in our model (Fig. 1). The graph can be converted to the matrix equation:

$$
\begin{bmatrix} n(\text{EPY}) \\ n(\text{LPY}) \\ n(\text{J}) \\ n(\text{A}) \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & F_4 \\ G_1 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix} \begin{bmatrix} n(\text{EPY}) \\ n(\text{LPY}) \\ n(\text{J}) \\ n(\text{A}) \end{bmatrix}_t
$$

or $\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$, where $\mathbf{N}_t$ and $\mathbf{N}_{t+1}$ are the population size vectors at time t and time $t + 1$ respectively, and $\mathbf{A}$ is the transition matrix. We assumed density-independent population growth, and modeled only the female population, assuming that there were enough males to fertilize all females. The program STAGE-COACH (Cochran and Ellner 1992) was used to calculate the finite rate of increase (λ), and sensitivities and elasticities of λ to variation in the elements of $\mathbf{A}$ (DeKroon et al. 1986, Caswell 1989), as well as other key age-based demographic parameters (Cochran and Ellner 1992). An approximate standard error was calculated for λ using the following formula (Lande 1988, Caswell 1989):

$$
V(\lambda) \approx \sum_{i,j} \left(\frac{\partial \lambda}{\partial a_{ij}} \right)^2 V(a_{ij})
$$

where $V(\cdot)$ is the variance in a parameter, λ is the finite rate of increase, a_{ij} is the matrix element in the ith row and the jth column of $\mathbf{A}$. Fertility is a composite parameter derived from fecundity, sex ratio, adult survival, and offspring survival (Caswell 1989). The sensitivity and elasticity of λ to variation in the parameters that make up fertility (F_4) was calculated by differ-
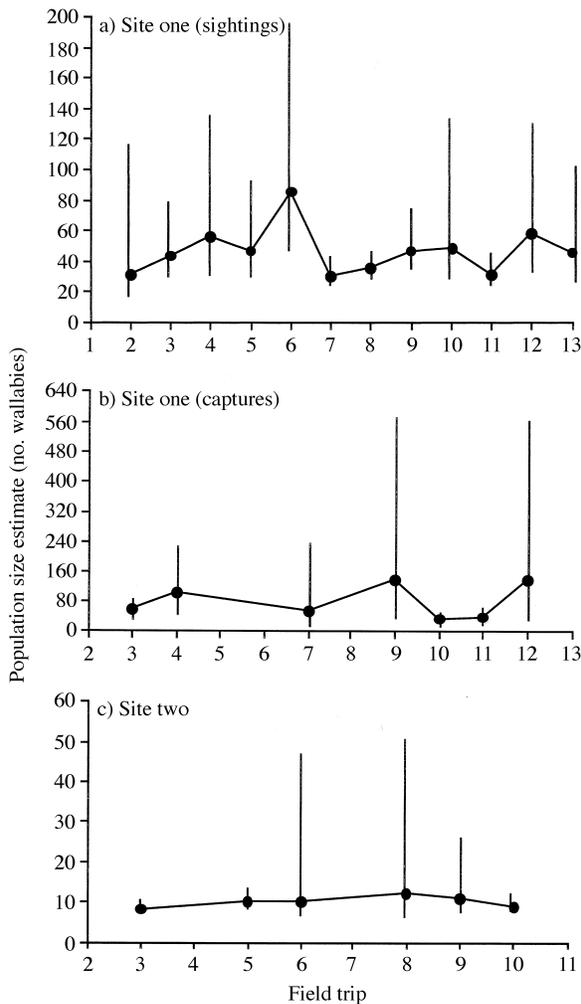
FIG. 2. Population size estimates with 95% confidence intervals for each field trip, based on (a) mark–resight records of radio-tagged wallabies at site one (JHE method), (b) mark–retrap records at site one, and (c) mark–retrap records at site two. Estimates based on captures could not be calculated for some field trips, because there were no recaptures within a trip.

entiating the elements of **A** with respect to each parameter, applying the chain rule for differentiation, and then summing over all elements:

$$\frac{\partial \lambda}{\partial x} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}.$$

The calculation of these sensitivities, elasticities, and the standard error for λ were performed using MATLAB 5 (Math Works 1997).

RESULTS

Population size and density

None of the three methods used to detect population size changes (closed population estimates from trapping data, from resighting radio-tagged wallabies, or density estimates from line-transect counts) showed statistically rigorous evidence of a population increase at either site, because the confidence intervals were usually very large (Figs. 2 and 3). The intrinsic rates of increase (r) based on capture data were close to zero ($r = 0.002$ for site one and $r = 0.008$ for site two), whereas the values based on resightings and line-transect estimates at site one were strongly positive ($r = 0.30$ and $r = 0.18$, respectively). Power analysis showed that there was a 58% chance of detecting a 28% change annually in the population of site one with this line-transect sampling regime. In order to detect a change in the population with 95% certainty, the number of field trips over three years would need to be increased from 12 to >18, or the population would have to be growing at >57% per year.

The estimates of mean population size at site one from capture–recapture data (40 wallabies) and from capture–resight data (47 wallabies) were consistently larger than at site two (13 wallabies; Fig. 2). Because of very low sample sizes, we did not attempt to estimate population density at site two using the line-transect method. However, the population estimate divided by the total area used by all radio-tagged wallabies at site two gave density values of 3.4–11.3 wallabies/km², which was also consistently lower than the line-transect estimates of density at site one of 11.7–32.2 wallabies/km² (Fig. 3). The area sampled by line-transect counts was ~4.5 km², so the mean population estimate from line-transects was 83 wallabies.

Correlates of survival and trapability vs. sightability

The initial goodness-of-fit tests in RELEASE suggested that the capture–recapture data were not affected by violations of the assumptions. The capture–resighting data, however, failed the goodness-of-fit test (test 2 of RELEASE, $\chi^2 = 7.31$, df $= 14$, $P = 0.016$), which indicates that newly released animals did not have the same probability of being seen or surviving as did earlier releases. This test usually fails if there are behavioral or survival responses to captures or sightings (Burnham et al. 1994). Closer examination of the time
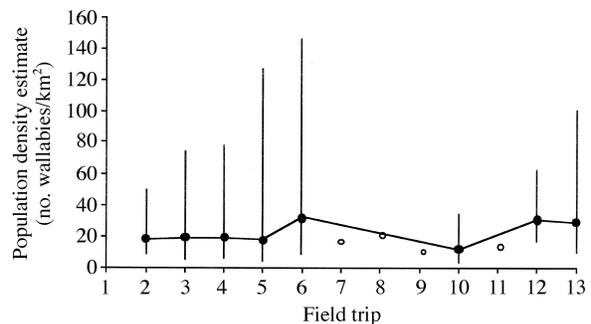

FIG. 3. Population density estimates with 95% confidence intervals for each field trip, based on line-transect counts at site one. Open circles represent mean estimates for which 95% confidence limits were 0, >1000.

TABLE 1. Results of the CJS survival (ϕ) and capture probability (p) model for adult bridled nailtail wallabies based on (A) captures for both sites; (B) sightings for site one, November 1993–September 1995; and (C) sightings for site one, November 1995–November 1996. The final model is shown in boldface.

Hypotheses tested				AICc	Likelihood ratio tests		
Factors affecting survival (ϕ)	Factors affecting capture probability (p)	Par†	ΔAICc‡	weight§	χ^2	df	P
A) Captures for both sites							
Saturated	saturated	84	153.02	0.00			
Constant	food + sex + site	5	12.81	0.00	34.4	10	0.00
Constant	sex + site $\times$ time	24	7.18	0.01	13.6	9	0.17
Constant	sex + time	14	14.11	0.00	16.3	1	0.00
Constant	site + time	14	1.14	0.14	3.36	1	0.07
Constant	sex + site	4	10.80	0.001	34.4	11	0.00
Month	sex + site + time	18	4.67	0.02	2.10	3	0.55
Year	sex + site + time	17	4.21	0.03	0.29	2	0.87
Constant + rain	sex + site + time	16	1.92	0.09	0.32	1	0.57
Constant + dingoes	sex + site + time	16	1.04	0.15	1.20	1	0.27
Constant + forbs	sex + site + time	17	3.06	0.05	1.44	2	0.49
Constant	**sex + site + time**	**15**	**0.00**	**0.25**			
B) Sightings for site one between November 1993 and September 1995							
Saturated	saturated	26	29.61	0			
Month + rain	time	11	2.42	0.07			
Month + year + rain	time	12	4.64	0.02			
Constant	time $\times$ sex	15	11.67	0.00	5.95	8	0.65
Constant	constant	2	4.96	0.02	15.4	5	0.01
Constant + year	time	8	2.01	0.08	0.13	1	0.72
Constant + food	time	8	2.02	0.08	0.12	1	0.73
Constant + dingoes	time	8	1.53	0.10	0.60	1	0.44
Const + rain	time	8	1.51	0.10	0.63	1	0.43
Const + month	time	10	0.23	0.20	6.23	3	0.10
Constant	**time**	**7**	**0.00**	**0.22**			
C) Sightings for site one between November 1995 and November 1996							
Saturated	saturated	14	13.91	0.00			
Constant	time + sex	5	2.98	0.09	5.18	1	0.02
Constant	constant	2	6.18	0.02	14.8	4	0.01
Constant	time	4	2.20	0.14	6.58	2	0.04
Constant + rain	time $\times$ sex	7	1.66	0.18	0.59	1	0.44
Sex	time $\times$ sex	7	2.00	0.15	0.24	1	0.62
Constant	**time $\times$ sex**	**6**	**0.00**	**0.42**			

† The number of estimable parameters for each candidate model.
‡ The change in AICc at each step.
§ The relative probability that the model is correct.

periods affected showed that the anomalous data occurred in late 1995, at around the time when vegetation conditions improved markedly (Fisher 1999*b*). We therefore divided the data into two periods for analysis of survival (November 1993 to September 1995 and November 1995 to November 1996). For these data sets, the goodness-of-fit tests failed to reject the null hypothesis that the assumptions were met, but the data were sparse.

The final CJS model based on trapping data did not reveal any difference in survival rates between study sites, sexes, or times, but all three variables affected the probability of capture (Table 1A). The survival estimate using trapping data was 0.80 (95% CL = 0.75, 0.84) per 3 mo, which is an annual survival rate of only 0.41. Capture probabilities were consistently higher for females than for males, and for animals at site two than for animals at site one. Capture probabilities also varied over time, but not according to a regular

seasonal pattern. The lowest (0.15, 0.18, and 0.16) were for males at site one between November 1993 and March 1994, between March and July 1995, and between September and November 1995. The highest (0.82) was for females at site two between September and November 1994 and between July and September 1996.

The model based on sighting data for the period up until September 1995 indicated that survival did not vary between groups or times, but that sighting probability depended on time (Table 1*b*). The survival rate from sighting data for this period was 0.89 (95% CL = 0.84, 0.93) per 3-mo interval, which corresponds to an annual estimate of 0.70. The sighting probabilities for this period varied between 0.72 (September–November 1994) and 1.0 (June–September 1994). The sighting data for 1996 also indicated that survival was constant, but the survival estimate was very low: 0.72 per 3-mo period (95% CL = 0.63, 0.79), corresponding

TABLE 2. Demographic parameters and sensitivity of population finite rate of increase (λ) to changes in each parameter.

Parameter	Estimate	n	Effects on λ Sensitivity§	Elasticity‖
Early pouch young survival†	0.93 ± 0.19	40	0.007	0.006
Late pouch young survival†	0.82 ± 0.34	43	0.08	0.06
Juvenile/young-at-foot survival‡	$0.47 \pm 0.14–1.0$	15	0.14	0.06
Annual adult survival‡	$0.80 \pm 0.64–0.97$	55	0.80	0.74
Female annual fecundity†	3.1 ± 0.16	27	0.02	
Proportion of female births†	0.51 ± 0.07	26	0.13	

† Mean ± 1 SE, calculated from recaptures of females on consecutive field trips; SE values indicate variability between individual females (Fisher 1999*a*).

‡ Mean and 95% CI from Cox's proportional-hazard model based on radio-tagged animals.

§ Sensitivity is the effect on λ of a small additive change in the vital rate.

‖ Elasticity is the relative effect on λ attributable to a small proportional change in one of the stages in the projection matrix.

to 0.27 per year. Data were sparse, and some sighting probabilities could not be estimated. However, male and female sighting probabilities varied differently from each other over time, indicating that behavioral responses to environmental conditions for each month differed for each sex. The highest sighting probabilities for both sexes in 1996 were for the interval March–July ($P = 1.0$). From November 1995 to March 1996, the probability of seeing males was only 0.65, whereas the probability of seeing females was 0.84. For radio-tagged adults, mean annual survival was estimated to be 0.80. Survival of juveniles was significantly lower than that of adults ($\chi^2 = 15.65$, $P = 0.0001$, Table 2, Fig. 4).

Population dynamics and life history parameters

The projection model indicated that the population was increasing at 28% a year, but that λ had a large standard error that included 1, so the population could have been stable (Table 3). Elasticities showed that λ is far more sensitive to changes in adult survival than to changes in other vital rates. In absolute terms (i.e., according to sensitivities), adult survival had the greatest effect on λ, followed by juvenile survival and birth sex ratio, but λ was robust to changes in birth rate and
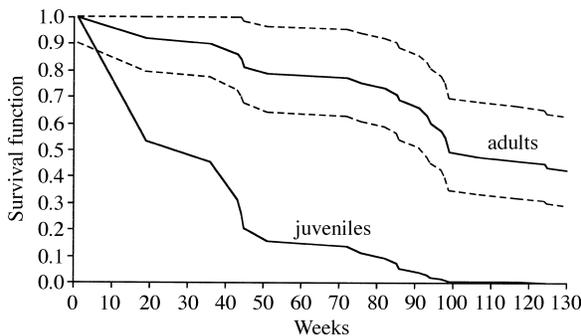

FIG. 4. Cox's proportional-hazard regression functions for adults vs. juveniles, based on radio-tagging data. The mean survival function curve for adults is shown with 95% confidence limits.

pouch young survival (Table 2). The projected mean life-span was 5.8 yr.

DISCUSSION

Population size and density

The maximum density estimate of 32 wallabies/km² is lower than values of 60–90 reported for other species of small and medium-sized macropods such as hare wallabies, *Lagostrophus fasciatus* and *Lagorchestes hirsutus*, tammar wallabies, *Macropus eugenii*, and red-necked wallabies, *M. rufogriseus* (Inns 1980, Johnson 1987, Short and Turner 1992), and there is anecdotal evidence that the population density of bridled nailtail wallabies at Taunton National Park was much higher than this current estimate in the 1980s (Gordon and Lawrie 1980, Tierney 1985). Line-transect counts carried out by managers throughout the park since December 1991 also suggest that the population halved between 1991 and 1995, although confidence limits for these estimates are very high (G. Porter and L. Pitt, *unpublished data*). The mean density of bridled nailtail wallabies estimated from these data is 8 wallabies/km², which is a similar value to the lowest density estimates in our study. Monitoring between 1993 and 1998 also indicates that population trends were correlated with rainfall (Lundie-Jenkins et al. 1998). Given that numbers almost certainly declined during the 1991–1995 drought, and that this species has a high reproductive rate (Johnson 1997), we expected the population to recover when conditions improved.

The three methods used to estimate population size showed that the population size and density at site one were greater than at site two, and that there was indeed a positive trend in abundance for values based on re-sightings of radio-tagged wallabies and line-transect estimates. However, none of these methods individually was adequate to detect changes in abundance in a statistically rigorous way. Mean population size estimates varied from 40 to 83 at site one, and absolute estimates based on capture–recapture and capture–resight data were affected by negative bias. The most

TABLE 3. Results of the matrix projection model based on age-class-specific survival and fertility parameters from Table 2.

Parameter name	Time	Estimate (mean ± SE)
Finite rate of increase, λ	per 2 months	1.04 ± 0.068
Finite rate of increase, λ	per year	1.33 ± 0.408
Intrinsic rate of increase, r	per year	0.28 ± (−0.08–0.55)

likely reason for this bias was that aspects of the behavior of the wallabies did not conform to the assumptions of the closed-population mark–recapture models.

Absolute values of population size derived from captures had large confidence intervals, and were very likely to be negatively biased by the unequal capture probabilities among times, sexes, and sites (Fig. 2). Model selection procedures in the program CAPTURE compensate for unequal capture probabilities, but estimates are nevertheless negatively biased when there are highly unequal capture probabilities, and the degree of bias is correlated with sample size (White et al. 1982, Hallett et al. 1991, Koper and Brooks 1997). White et al. (1982) recommend that, for population sizes <100, capture probability should be at least 0.3 for this method to be reliable. According to the CJS models, the probabilities of seeing individual wallabies and capturing females were adequate, but the probability of capture was often below 0.3 for males.

On the other hand, simulations have shown that the JHE method of combining Lincoln-Petersen estimates is expected to be slightly positively biased if there are low sighting probabilities and small sample sizes (Neal et al. 1993, White 1993). However, Bartmann et al. (1987) found that abundance estimates using this method for a confined population of deer were negatively biased. They suggested that >45% of a small population should be marked to obtain reliable estimates. The percentage of radio-tagged bridled nailtail wallabies at site one probably varied between 10% and 20%.

The most serious problem for all of the abundance estimation methods was that wallabies altered their habitat use according to pasture conditions, increasingly avoiding open areas when conditions improved (Fisher 1999a). This had the same negative-biasing effect on capture–recapture, sighting, and line-transect estimates as if a large section of the population had died or become permanently trap shy. Variation in the feeding-site preferences of the wallabies was also a source of bias in the line-transect estimates, because habitat around the transect lines was not representative of the site as a whole. Use of tracks is discouraged for line-transect methods because they do not sample habitat randomly (Buckland et al. 1993). In this study, managers deliberately created pasture areas along tracks, and tracks ran alongside cleared paddocks at the edge of the park. Wallabies fed near the tracks during the drought, and shifted their feeding areas to habitat under cover as conditions improved (Fisher

1999a). These factors are likely to result in a positive bias in population estimates in drought years, and negative bias in high rainfall years. This is a potential problem, because movement into the open to find food could reduce the chance of detecting a decline.

The most important assumption of line-transect counts, that animals on the transect lines are not missed (Buckland et al. 1993), was likely to be correct because of the antipredator behavior of the wallabies (i.e., freezing, crouching, or fleeing a short distance; Fisher 1998), and the high visibility of the reflective ear tags. The mean population estimate at site one derived from line-transect counts was 83, which is almost twice as high as that derived from captures and sightings. Although the placement of transect lines was not ideal, line-transect estimates appeared to be the least negatively biased method, with the exception of models based on radio-tracking. Useful long-term trends can be assessed with the line-transect method, but short-term trends and absolute estimates of abundance are unlikely to be reliable.

Survival

The probability of trapping and sighting adults varied among times, sexes, and sites, but the probability of survival did not (Fig. 2). This was despite differences in body size, growth rate, and ranging behavior between the sexes (Fisher and Lara 1999), and differences in the habitat and population density between the sites. The annual survival estimate from sighting data was 70% for 1994–1995, and 27% for 1996; the total estimate from capture data was 41%, and the total estimate from radio-tagging data was 80%. As for the abundance estimates, the causes of disparity between these values are likely to be violations of the models' assumptions due to variation in habitat use and apparent behavioral response to trapping.

The general assumptions of capture–mark–recapture modeling are that animals are representative, tagging does not affect survival, there is no tag loss, capture and release occasions are brief, unknown emigration is permanent, fates are independent, and groups have homogeneous survival and capture probabilities (Burnham et al. 1987). All of these assumptions appeared to be met for the CJS analysis of bridled nailtail wallaby adults. A high percentage of the population was tagged (30–80% of individuals seen), there was no tag loss, and trapping sessions lasted 1 wk, with 3-mo intervals between periods. For the CJS model, goodness-of-fit tests confirmed that there were no violations of the

latter three assumptions (Burnham et al. 1994). Despite this, survival estimates were very low, except for the estimate based on capture–resighting data for 1994 and 1995.

The assumptions of the Cox's proportional hazards model require that animals are representative, fates are independent, and survival is monitored continuously. Most importantly, the censoring mechanism should be random, which means that the cause of collar failures must be unrelated to causes of death (Pollock et al. 1989). These assumptions appear to have been met; deaths were registered weekly, dingoes did not destroy transmitters, and there was no poaching. The survival estimate based on radio-tagging data was the only one that was unaffected by habitat use and behavior variability. For this reason, we considered survival estimates derived from radio-tagging data to be the most accurate, and used these for the population model.

Population dynamics

Taylor and Gerrodette (1993) have argued that, for rare species, modeling population dynamics using data on age-specific survival and fecundity may be a more powerful method of assessing population trends than abundance estimation. We used a matrix population projection model to investigate population dynamics of bridled nailtail wallabies, based on the best survival and fecundity estimates available. This type of model is deterministic, and relies on identification of biologically meaningful life history stages (Caswell 1997). It is also assumed that the fates of individuals within a stage class are identical. However, the extent to which errors in parameter estimates will affect the conclusions can be inferred from the elasticity values (Crouse et al. 1987). In this study, adult survival was both least variable and had the highest elasticity values. This is to be expected if the higher variation in juvenile survival was real, rather than only being due to sample size, because there is generally a strong negative correlation between the relative effect of vital rates on population growth rate and variance over time, perhaps due to selection pressure to minimize variability of λ (Pfister 1998).

The projected intrinsic rate of increase was very high (28% per year; Table 3), and similar to values obtained from sighting data (30%), although the standard errors were large enough that the population could have been stable or even decreasing slightly. For bridled nailtail wallabies, the rate of population increase, λ, was most sensitive to changes in adult survival. This pattern is typical of relatively long-lived species, such as large mammals (Goodman 1981, Brault and Caswell 1993). It implies that if it is possible to improve adult survival by reducing the effects of dingo predation, then this will be the most effective management strategy. Both the elasticity and variance of vital rates are important to the interpretation of population models for conservation (Caswell 1997, Wisdom and Mills 1997). Var-

iations in λ can also be closely associated with life cycle stages having high variability, even if the elasticities of these stages are lower, because it may be easier to change the more variable parameters (Noon and Biles 1990). This suggests that an effective management strategy would also be to reduce predation on juveniles by controlling cats, because juvenile survival was highly variable. Increasing the production and survival of pouch young would have the least effect on λ, and would be very difficult to achieve. Matrix projection models only consider the effects of changes in one parameter at a time (Caswell 1997), and cannot predict the effects of multiple changes concurrently, so we cannot address multiple management strategies with this method.

Conclusions

The estimated values for mean abundance were very low: ~100 individuals at the two study sites. These sites are the only areas where bridled nailtail wallabies were regularly seen during the study. Survival rates of adults and pouch young were higher than those of juveniles (young-at-foot). Three of the four methods of analyzing population dynamics (mark–resight, line-transect estimates, and matrix projection models) indicated a positive trend in abundance after the drought. Mark–retrap methods showed no trend and were least useful. Calculating λ from survival estimates obtained by radio-tracking is the most effective way to monitor population dynamics of bridled nailtail wallabies. Our findings are also likely to apply to other solitary, nocturnal, medium-sized species that rely on cover to avoid predators and so vary their behavior according to cover availability. We recommend the distance-sampling method for long-term monitoring in this case, however. Firstly, it gave the least biased absolute values of abundance; secondly, it would be impractical to monitor population dynamics using radiotelemetry in the long term; and thirdly, it is non-invasive and inexpensive. For the conditions encountered in our study, λ was most sensitive to changes in adult survival. Decreasing predation on adults by controlling dingoes is likely to be an effective strategy to increase population growth.

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