

Matthew Clarke · Yew-Kwang Ng

# Population dynamics and animal welfare: issues raised by the culling of kangaroos in Puckapunyal

Received: 28 June 2004 / Accepted: 30 November 2005 / Published online: 29 April 2006  
© Springer-Verlag 2006

**Abstract** The culling of kangaroos at the Puckapunyal Army base (Australia) raises some intriguing ethical issues around animal welfare. After discussing the costs and benefits of the cull, this paper addresses the more general animal welfare issues related to population dynamics. Natural selection favours the maximization of the number of surviving offspring. This need not result in the maximization of the welfare of individuals in the species. The contrast between growth maximization and welfare maximization is first illustrated for a single population and then discussed in terms of competing populations. In the Lotka-Volterra model of competing species and its generalizations, the choice of different birthrates does not affect the population sizes at equilibrium. Welfare could be much higher at lower birthrates without even reducing numbers (at equilibrium).

## 1 Introduction

On May 16, 2002 the Victorian State Government Department of Natural Resources and Environment issued a permit for the culling of 15,000 kangaroos at the Australian Defence Force army base at Puckapunyal in central Victoria. An estimated 80,000–100,000 kangaroos lived within this fenced 44,000-ha site. This number was unsustainable with the majority of kangaroos starving and ill. This paper is interested in using this practical real life example to re-examine a number of welfare economic concepts primarily related to population dynamics. This examination relies on the consideration of the Puckapunyal kangaroos as affective sentient beings whose welfare can be treated in a similar manner as humans (Singer 1975,

---

M. Clarke (✉)

School of Social Science and Planning, RMIT University, GPO Box 2476V, Melbourne, VIC 3001, Australia

E-mail: matthew.clarke@rmit.edu.au

Y.-K. Ng

Department of Economics, Monash University, Melbourne, Australia

2000). As with humans, the welfare of affective sentient animals is happiness minus suffering (Ng 1995).<sup>1</sup>

Sentients are usually defined as beings that are capable of subjectively perceiving or feeling by means of the senses. This includes not only being capable of the feeling of being happy and/or unhappy, but also includes beings just capable of perceiving things without having any affective feelings. Thus when discussing welfare impacts on animals, it is important to further classify sentient animals into affective sentients or non-affective sentients (Ng 1995). Kangaroos are affective sentient beings. They have the capacity to feel pain and pleasure. It is possible and reasonable therefore to rank various social states in terms of the welfare effects on these beings.

Whilst a number of welfare issues are briefly reviewed, particular attention is paid to population dynamics and how this affects welfare maximization. Similar consideration is limited within the literature. Blackorby and Donaldson (1984, 1992) discuss the ethics of animal exploitation in research and food production, particularly examining the implication of these activities and apply their own ethical principle of critical-level utilitarianism. In contrast to classical or ordinary utilitarianism, critical-level utilitarianism maximizes the sum of individual (or affective sentient, when generalized to cover animals) utilities in excess of a certain positive critical level. Blackorby and Donaldson (1984) use critical-level utilitarianism to solve the well-known moral philosophical problem of optimum population. Classical utilitarianism maximizing aggregate utility/welfare may prefer an arbitrary large number of the population with a tiny but positive level of average welfare to a small population with a high level of average welfare (called the repugnant conclusion; see Parfit 1984; more on this point below). In contrast, the maximization of average welfare implies the unreasonable rejection of adding very happy individuals of slightly lower welfare than the existing people. For an alternative solution of this dilemma, see Ng (1989). However, Blackorby and Donaldson (1984) and Ng (1989) consider comparative static comparisons rather than the population dynamics discussed in the main Sect. 4 of this paper.

## 2 Puckapunyal and the kangaroo cull

The Australian Defense Force army base at Puckapunyal in central Victoria is a 44,000 ha site. To protect against purposeful or inadvertent intrusion, Puckapunyal is surrounded by a number of secure perimeter fences. Whilst the purpose of these fences is to keep unauthorized visitors out, they also keep wildlife locked in. Much of Puckapunyal is bushland (left purposely so for military training purposes) and contains natural fauna and flora. Kangaroos are amongst the wildlife found in Puckapunyal. Central Victoria endured a long drought through the late 1990s and early 2000s. Due to the perimeter fence surrounding Puckapunyal, the kangaroos (and other species) inside were unable to follow natural migration patterns to better feeding grounds. Over a period of time, the kangaroo population completely razed

---

<sup>1</sup> In contrast to the case of humans, it is less controversial to view animal welfare hedonistically (in the philosophical sense instead of the everyday usage of this term) as the balance of happiness over suffering. Even for human, a case for viewing welfare just as net happiness can be made (Kahneman et al. 1997; NG 2000a).

all vegetation within Puckapunyal and was left without sustainable food stocks. Illness and starvation followed.

A sustainable population within the Puckapunyal base is estimated to be 40,000 kangaroos (about one kangaroo per hectare). However, at least twice that number, and possibly more, were alive in the period leading up to the cull announcement in May 2002. Given the limited space, overpopulation led to the starvation and suffering of a large number of kangaroos.

### 3 Measuring net benefits to social welfare of the cull

As a result of insufficient food supply, caused by overpopulation within a confined space, up to 100,000 kangaroos at Puckapunyal were in various stages of starvation, illness and misery. As affective sentient beings, all kangaroos were experiencing reduced welfare as this situation continued. The Victorian State Government Department of Natural Resources and the Environment, in conjunction with the Australian Defence Force, issued a permit to cull 15,000 kangaroos in May 16, 2002. (A second and final permit for an additional cull of kangaroos was issued in September 2002). The expected outcome was that this judicious killing, in combination with the natural death of an additional 20,000 kangaroos through starvation, would lower the population to more sustainable levels.

The culling of kangaroos had an immediate impact on the present and future welfare of those surviving. Due to the reduced pressure on resources, surviving members had greater welfare. It is possible to consider the welfare affects caused by the cull in a similar way to Broome's (2001) analysis of the effects of an epidemic on welfare. This welfare test is dependent upon the assumption of intertemporal well-being being measurable on a cardinal scale, and being comparable across time. This analysis considers different sets of "potential" kangaroos. A "potential" kangaroo is one that exists in some state or another. This set is assumed to be countable. In each state, some "potential" kangaroos exist and others do not. It is further assumed that each state contains a finite number of kangaroos, each of whom live for a finite period. This avoids the problems of infinite sums. Finally, the value of non-existence is set at zero welfare. Aggregate welfare, requires the addition of the welfare levels of all members of that population under study across all time. This requires addition across two dimensions – time and affective sentient beings (Broome 2001).

Within this assumed scenario, the death and non-birth of two kangaroos is considered a loss to total welfare as 'death is bad – at least partly – because it deprives its victims of all the good things she would have enjoyed in the rest of her life' (Broome 2001, p. 96). It should be noted though that death may be preferable if living resulted in suffering without hope of escape. Zero welfare may be an attractive alternative to a large amount of negative welfare. Apart from non-existence, zero welfare applies when the amount of positive enjoyment is offset by that of negative suffering (Kahneman et al. 1997; NG 2000a). However, at least for the case of humans, killings have obvious enormous negative implications for the wider society. This is evidenced by the banning of homicide which can be justified even on purely utilitarian grounds.

Within this approach we have assumed separability of affective sentient beings in order to calculate total welfare, but in doing so we implied 'not only that

we can evaluate a... life independently of how things go for other... (affective sentient beings), but also that the value of... existence is independent of how many other(s)... exist and of how things go for them' (Broome 2001, p. 99). It is important to note the distinction between the independence between utility/welfare values and separability. The former refers to the independence of the utility/welfare level of an individual of the objective variables (such as consumption/income) of other individuals and is clearly not realistic and can be justified only on the grounds of simplicity. The latter (separability) refers to the compelling principle that social valuation of an individual's well-being should be independent of the well-being levels of others as individual well-being levels are already ultimate (Ng 2000b).

However, issues of non-separability or non-independence must also be considered as they do affect the compellingness of separability discussed above. The welfare of one kangaroo can be affected by the welfare of another. In one instance, one kangaroo might be disabled through the death of its parent resulting in its lower welfare and in the second, a kangaroo that would have been born, is not because of the death of its parents. This implies a "restricted" domain, which restricts utility distributions to ones that are "natural" in that they reflect hereditary order. This further implies that the underlying domain has a tree structure, thus supporting the assumption of separability.

A cull is accepted therefore if it increases total welfare, accepting that total welfare includes the welfare (or lack thereof) of both the present generation and future generations. This requires incorporating social discounting. The social discount rate can either be negative ( $< 0$ ), positive ( $> 0$ ) or neutral (0). If the social discount rate is negative, future generations are given greater weight, if positive, the present generation is considered more important, and intergenerational equality is captured with a neutral or zero social discount rate. For subjective values, such as well-being, and in the absence of non-survival to realize the future welfare values, the only valid discount is neutral or zero discount.

If the objective function of society is to maximise welfare, it is possible that by removing some members of that group with low levels of happiness (perhaps through starvation or illness), this will immediately increase the average level of welfare for that group. 'This involves not only some technical details but also raises the intriguing questions as to whether average or total welfare (i.e. average welfare per individual times the number of individuals) should be maximized and if the former, average of what time period' (Ng 1995, p. 273). Further, by reducing the numbers of the group, natural resources are increased and made available for consumption by the remaining members also increasing their welfare. Thus the outcome of removing affective sentients with low-level welfare is twofold.

The question of how low must an affective sentient's welfare be before death is a preferred alternative for both that being and other members of society must be raised. 'At least from the viewpoint of welfare maximization (which could be argued to be the rational objective; see Ng 1989), a life is only worth living if welfare is positive' (Ng 1995, p. 269).<sup>2</sup> Within these circumstances, the alternative social state includes the killing of certain members of society. Within the Puckapunyal

---

<sup>2</sup> Ng's view that any positive welfare involves a life worth living is not consistent with the resolution of the paradox of average versus total welfare maximization by using the critical-level utilitarianism as discussed above. However, as noted there, Ng has alternative resolution of this paradox.

cull there was a code of practice for the killing of kangaroos. This included head or heart shots, with a focus on distressed, emaciated and injured animals in the most densely populated areas.

## 4 Population dynamics

Given the finite space at Puckapunyal (due to its secure fencing), it is expected that over population will occur again in the future. Population control is therefore a central issue in understanding how to maximize welfare (or minimize misery) of kangaroos in this environment. The following discussion presents an initial treatment of how population dynamics of non-human affective sentient beings can be conceptualized.

### 4.1 A simple population in exponential growth

We first consider the simple case of a single population not limited by any resource constraint and growing exponentially. That growth maximization as might be favoured by natural selection need not be (total) welfare maximizing can be shown most simply by distinguishing only between those that die before leaving offspring and those that do leave offspring. Other aspects such as differential fertility, generation length, age structure, sex, etc. are ignored. It is true that natural selection need not always result in 100% growth maximization. However, since natural selection is based on fitness in terms of survival and propagation, it has a bias away from welfare maximization towards growth maximization. For simplicity of analysis, we examine only these two contrasting cases.

Suppose natural selection has resulted in each mature adult bearing ten offspring of which three survive to adulthood to give the next generation of offspring. The (asexual) population is then trebled every generation, a phenomenal rate of growth. However, this spectacular growth in number may also be a growth in misery. For example, suppose that each individual who survives to bear offspring derives a lifetime welfare level of two units and each individual who does not survive until adulthood derives a lifetime welfare level of  $-1$  unit. Then, for the ten offspring of an adult, their aggregate welfare is  $(2 \times 3) - (1 \times 7) = -1$ . Starting from any given initial population size (e.g. 10), this negative aggregate welfare explodes exponentially as the population trebles after each generation (e.g.  $-10, -30, -90, -270, -810, \dots, -34, 867, 844, 010$  after only 20 generations).

On the other hand, suppose that, by lowering birthrate per adult from ten to five, the number of individuals surviving to adulthood drops from three to two. Then, the population only doubles (instead of trebles) each generation. For the five offspring of an adult, their aggregate welfare is  $(2 \times 2) - (1 \times 3) = +1$ , even assuming that the welfare levels of an adult and a minor have not been increased. Instead of a negative aggregate welfare for the offspring of any given adult, we now have a positive aggregate welfare. This positive welfare also grows exponentially, doubling every generation (e.g. 10, 20, 40,  $\dots, 10,485,760$  after only 20 generations). This exponential growth in positive welfare accords more with welfare maximization than the exponential growth in misery in the case of possibly growth

maximization as might be the result of natural selection described in the preceding paragraph.

For the simple case of a single population growing exponentially discussed above, the per generation growth rate  $g$  is simply described by

$$g = bs - 1, \quad (1)$$

where  $b$  is the number of births per adult and  $s$  is the proportion of those who survive to adulthood to contribute to the next round of births. Obviously,  $s$  is a (usually decreasing, except at very small values of  $b$ ) function of  $b$ . Maximizing  $g$  with respect to  $b$  (taken as continuous to facilitate the use of calculus), we have

$$s + b \frac{\partial s}{\partial b} = 0, \text{ or } \eta = 1 \quad (2)$$

as the condition for growth maximization, where  $\eta \equiv -(\partial s / \partial b)b/s$  is the reduction in the survival rate with respect to an increase in births, in proportionate or elasticity form.

For welfare maximization, the present writers are in favour of the maximization of total welfare (though time discounted for the uncertainty of future welfare being actually realized). However, many people are in favour of the maximization of average (over the number of population concerned) welfare. This issue of the total versus the average principle has plagued moral philosophers and economists for a long time. Though Ng has argued for the normative compellingness of the total principle elsewhere (Ng 1983, 1986, 1989), we do not propose to engage in this controversy here. Instead, both average and total welfare maximizations are discussed.

Let the life-time welfare level of a typical individual who survives to adulthood be  $a$  and that of one who does not survive (i.e. one who dies in childhood) be  $c$ . For simplicity, these values are taken to be independent of  $b$  and remain constant through time. The average welfare for any generation is then described by

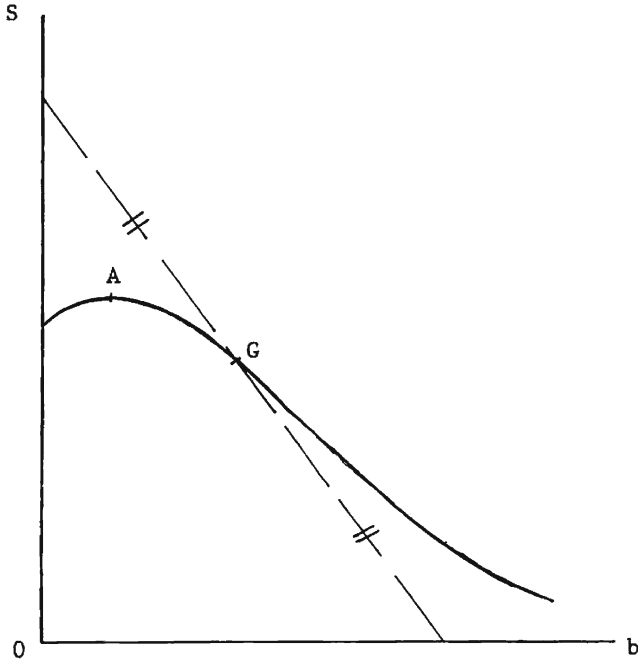
$$sa + (1 - s)c. \quad (3)$$

Maximizing (3) with respect to  $b$ , we have

$$(a - c) \frac{\partial s}{\partial b} = 0 \quad (4)$$

which requires  $\partial s / \partial b = 0$  unless  $a = c$ . Assuming reasonably that  $a > c$ , we maximize average welfare by maximizing the survival rate  $s$  at  $\partial s / \partial b = 0$ .<sup>3</sup> For  $s$  as a function of  $b$  indicated by the curve in Fig. 1 we have the average welfare maximization solution at the point  $A$  and the growth maximization solution at the point  $G$  (where the curve is tangent to a rectangular hyperbola).

<sup>3</sup> When kangaroos are starving, it may be the case that the starving adults have lower welfare than those who died young. However, in our simplified model here, we are only distinguishing between those who survive to adulthood and have offspring and those that died before having offspring. Moreover, we are only concerned with long-run comparisons, not with the special transitional periods of mass starvation. Thus, the assumption that  $a > c$  is acceptable.



**Fig. 1** Average welfare maximization (A) versus growth maximization (G)

It may be mistakenly believed that the principle of total welfare maximization involves just the maximization of

$$bsa + b(1 - s)c. \tag{5}$$

This maximizes the total welfare of the current generation but does not maximize total welfare through time since the population growth rate may differ. Since future welfare is involved, realization of which is uncertain, the appropriate objective function is the present value of the stream of (total) welfare through time discounted by an uncertainty discount rate. [Here, it is taken that the maximization of expected welfare in the presence of uncertainty is the right objective; see Ng (1984) for an argument in its favour.] Note that this differs from the interest rate or discount rate used by economists since it is unrelated to either the marginal productivity of capital or the time preference of individuals. Some economists are in favour of a zero rate of discount for the society and speak of irrational time preference due to “faulty telescopic faculty” (Pigou 1929, p. 25) arising from “weakness of imagination” (Ramsey 1929, p. 543) or from the “conquest of reason by passion” (Harrod 1948, p. 40). However, this ignores some degree of uncertainty in realizing future welfare. This uncertainty discount is in general a function of time and may also differ between species if the uncertainty involved differs. (However, if the uncertainty is mainly due to the destruction of the whole Earth by, say, celestial collision, it should be the same across species.) However, for simplicity, a constant rate is used. Similarly,  $b$ , the number of births per adult, may also change through time. Partly for simplicity and partly because changing  $b$  (say through genetic engineering in the future) is likely to be very costly and unlikely to be done frequently, we

take  $b$  to be independent of time. In other words, once chosen,  $b$  remains constant. The objective function for total welfare maximization is thus

$$W = \int_0^{\infty} \{sa + (1 - s)c\} N(0)e^{(bs-1-R)t} dt, \tag{6}$$

where  $R$  is the discount factor and  $N(0)$  is the number of population at time zero.

Assuming the convergence of the integral, integrate (6) to obtain

$$\frac{\{sa + (1 - s)c\} N(0)}{(1 + R - bs)}. \tag{7}$$

Maximizing (7) with respect to  $b$ , we have the following first-order condition (where  $s_b \equiv \partial s / \partial b$ ),

$$(s + bs_b)\{sa + (1 - s)c\} = (a - c)s_b(bs - 1 - R) \tag{8}$$

which simplifies to

$$(a - c)s^2 + \{(1 + R)(a - c) + bc\} s_b + sc = 0. \tag{9}$$

The above condition may also be obtained in the dynamic optimization problem of maximizing  $\int_0^{\infty} \{sa + (1 - s)c\} N(t)e^{-Rt} dt$  subject to  $\dot{N} = (bs - 1)N$  for the special case where  $db/dt = 0$ . Together with a specific function  $s = s(b)$ , (9) can be solved simultaneously for the optimal values of  $b$  and  $s$ . For example, if we have a simple linear

$$s = k - hb, \tag{10}$$

where  $k$  and  $h$  are constants, we may solve (9) and (10) to obtain

$$b = \frac{X \pm \sqrt{X^2 - 4(a - c)h^2 [(a - c)\{k^2 - (1 + R)h\} + ck]}}{2(a - c)h^2}, \tag{11}$$

where  $X \equiv 2(a - c)kh + 2ch$ .

For a specific set of values for the relevant constants, e.g.  $a = 1$ ,  $c = -1$ ,  $k = 1$ ,  $h = 1/5$ ,  $R = 0.3$ , we have the positive solution

$$b = 2, s = 0.6, W = 2N(0) \tag{12}$$

which contrasts with the growth maximization solution of

$$b = 2.5, s = 0.5, W = 0 \tag{13}$$

If  $R$  is sufficiently small, the integral in (6) does not converge. To maximize the objective function, the overtaking criterion may be used (Weizsäcker 1965). However, it is not believed that the present value of the relevant objective function can be infinite (Ng 1991). We live in a finite world. We integrate to infinity only because we do not know when the final day of our world (or the relevant species) will be. While a discount factor that makes the integral converge seems unduly big, this is only so because of the use of a constant discount factor. Ideally, we should



use a low discount rate for the immediate future when the continued survival of the species is more certain and a higher rate far into the future when continued survival seems much less likely (proportionately speaking, e.g. if the probability of surviving one thousand years is  $p$ , that of surviving two thousand years is less than  $p^2$ ). Secondly, when a long future is considered, a non-trivial exponential growth is almost certainly impossible. It is high time to move away from the simple case of exponential growth.

#### 4.2 Non-exponential growth

To move away from exponential growth, let  $s$  not only decrease with  $b$  but also decrease with  $N$ . (For many animal species,  $b$  itself also decreases with  $N$  as  $K$ , the “carrying capacity”, is approached. This complication is not considered here.) Consider a simple function where, for  $b\hat{s} > 1$  (otherwise no growth is possible),

$$s = \hat{s}(b) - \left\{ \hat{s}(b) - \frac{1}{b} \right\} \frac{N}{K}, \quad (14)$$

where  $s$ , a function of  $b$ , is the value of  $s$  when there is no density-dampening effect (i.e. when  $N$  approaches zero), and the parameter  $K$  is the carrying capacity determined by exogenous factors such as resources. For the purpose here,  $K$  is taken as a constant.

Since the population grows at the rate  $bs - 1$  per generation, we have, using a time period of the same length as a generation,

$$\frac{\dot{N}}{N} = (b\hat{s} - 1) \left( 1 - \frac{N}{K} \right), \quad (15)$$

where  $\dot{N} \equiv dN/dt$ . Since  $b\hat{s} > 1$ , it is clear from (15) that the population grows positively/negatively as  $N$  is smaller/larger than  $K$ . Solving the differential equation (15) for  $N$ , we have,

$$N(t) = \frac{K}{1 + \left\{ \frac{K}{N(0)} - 1 \right\} e^{(1-b\hat{s})t}}. \quad (16)$$

It can be seen that (15) and (16) are similar to the corresponding equations for logistic growth, except that the intrinsic rate of growth (usually denoted  $r$ ) is replaced by  $(b\hat{s} - 1)$  here. This is so since, from (14), if the density-dampening effect is absent (when  $N$  approaches zero),  $s$  equals  $\hat{s}$ . As the rate of growth equals  $bs - 1$ , the intrinsic rate of growth (i.e. the rate of growth in the absence of the density-dampening effect) equals  $b\hat{s} - 1$  (since  $s = \hat{s}$  here). However, in our formulation, by making the intrinsic and the actual rates of growth depend on  $b$ , rather than be equal to an assumed constant, we can analyse the question of the choice of  $b$  in a situation of logistic growth.

The value of  $N$  over time for different values of  $b$  as determined by Eq. (15) or Eq. (16) are illustrated in Fig. 2 for  $K = 1,000$ ,  $N(0) = 20$ , and  $N(0) = 1,500$ . For any given  $b$  (which also determines  $s$  and hence  $b\hat{s} - 1$ , the intrinsic rate of growth), the rate of growth depends on  $N$ , being positive if  $N < K$  and negative if

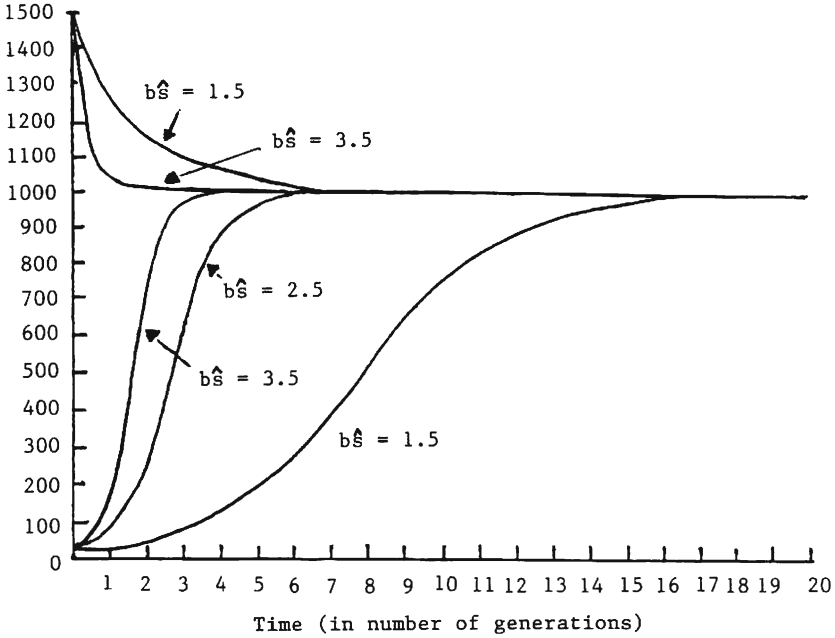


Fig. 2 Curve of population size as a function of time from Eq. (17), with  $K = 1,000$

$N > K$ . For any positive and non-negligible intrinsic growth rate (otherwise the population can hardly grow at all even without the density-dampening effect), the population quickly converges towards  $K$ , the carrying capacity. Here, the choice of  $b$  that maximizes the intrinsic growth rate can be seen to be rather pointless as the number of population [if commencing at  $N(0) < K$ ] cannot exceed  $K$  even if  $b$  assumes a value maximizing the intrinsic growth rate. The maximization of  $W$  (present value of total welfare through time) with respect to  $b$  can be analysed similarly as above (for the case of exponential growth) but the mathematics becomes more complicated.

A methodological question arises for average welfare maximization. In the case of exponential growth discussed above, for any value of  $b$ , average welfare remains constant through time. The maximization of average welfare thus gives an unambiguous solution at the point  $A$  in Fig. 1. However, for the present case of logistic growth, even given  $b$ , the value of average welfare changes through time since  $s$  changes with  $N$ . As average welfare varies with time, which average welfare should be maximized?

For a value of  $b$  that maximizes  $s$  (and hence average welfare) for the present generation, average welfare for future generations could be increased by a smaller  $b$  since this decreases the density effect through  $N$ . But this may be achievable only at a cost of a lower average welfare level for the present generation. There is a similar trade-off between different generations in the future. It might be suggested that the average (through time, perhaps discounted by uncertainty) of the average welfare levels be maximized. This seems to be a more acceptable (within the framework of average welfare maximization which the authors do not believe in)

objective if the relevant set of people is the same under alternative choices (of  $b$ ). In contrast, the choice of a smaller  $b$  referred to above, while making the welfare levels of future generations higher, may make these future generations different sets of people than if  $b$  were higher, since the choice of a different  $b$  may mean that different individuals would be conceived. Provided that the welfare levels of future generations remain positive, increasing the average welfare of the present generation may mean that all individuals are made better off and no one (except the unborn but prospective individuals) is made worse off. This paradox for average welfare maximization is similar to the paradox of resource exhaustion raised by Parfit (1984). Such paradoxes illustrate the unacceptability of ignoring the welfare of prospective individuals, individuals that could be born under one alternative but not yet actually born. For choices that involve that alternative, prospective individuals related to it cannot be ignored (Ng 1986). However, once we consider the welfare of prospective individuals, average welfare maximization can no longer be justified.

#### 4.3 The case of competing populations

The cull of kangaroos at Puckapunyal certainly would have affected other species as well. By reducing the number of kangaroos requiring food resources, other species will have greater food resources available to them.

Consideration can therefore be given interspecies welfare. If reducing the total kangaroo population by one increases the total welfare of another species relying on the same food resources, what is the optimal outcome? How can the welfare of one cohort of affective sentient beings be compared to the welfare of a second cohort of subspecies?

$$TW = \sum (K_{tw} + W_{tw} + \dots + O_{tw}), \quad (17)$$

where TW is the total welfare all affective sentient animals,  $K_{tw}$  is the total welfare of kangaroos,  $W_{tw}$  is the total welfare of wombats,  $O_{tw}$  is the total welfare of other affective sentient species.

Is it possible to value the welfare of one species above another? This could be done by allocating weights to certain affective sentient groups. Deciding what these weights should be though is not obvious.

$$TW = \sum (K_{tw} * \alpha_1 + W_{tw} * \alpha_2 + \dots + O_{tw} * \alpha_n), \quad (18)$$

where  $\alpha_1, \alpha_2, \dots, \alpha_n$  are the various weights for welfare.

As the real world is characterized by species competing with each other (for resources if for nothing else) with also predator-prey, symbiosis, and other relationships, we start from the most simple case of two competing species, the well-known Lotka-Volterra (L-V) model. We have

$$\frac{\dot{N}_1}{N_1} = r_1 \left( 1 - \frac{N_1}{K_1} - \alpha_{12} \frac{N_2}{K_1} \right), \quad (19)$$

$$\frac{\dot{N}_2}{N_2} = r_2 \left( 1 - \frac{N_2}{K_2} - \alpha_{21} \frac{N_1}{K_2} \right), \quad (20)$$

where a number subscript denotes the species,  $\alpha_{ij}$  is the competition coefficient on species  $i$  by species  $j$ , and  $r$  (the intrinsic rate of growth) may be replaced by  $b\hat{s} - 1$  if the choice of  $b$  is to be analysed.

Simple as it is, the L-V competition model has received strong support from laboratory experiments and field studies (e.g. see Roughgarden 1979, Chap. 21 and also Connell 1983; Schoener 1983, 1985 on summaries of relevant experiments; see also Cressman and Garay 2003; Edmunds et al. 2003; Gillespie 1998; Gordon 2000; Huang and Zu 2001; Turchin 2003). A most remarkable result of the model, a point to be emphasized here, is that the final or equilibrium outcome is determined only by the  $\alpha$ 's and  $K$ 's; and  $r$ 's (intrinsic growth rates, and hence birth rates  $b$ 's) do not enter into conditions determining different outcomes. For example, for the case where the final outcome is co-existence in a stable equilibrium illustrated in Fig. 3, the values of  $N_1$  and  $N_2$  at the equilibrium point is given by

$$N_1 = \frac{(K_1 - \alpha_{12}K_2)}{(1 - \alpha_{12}\alpha_{21})}, \quad (21)$$

$$N_2 = \frac{(K_2 - \alpha_{21}K_1)}{(1 - \alpha_{21}\alpha_{12})}. \quad (22)$$

The actual path and speed of movement towards the equilibrium outcome depend on the initial population sizes as well as  $r$ 's but the final equilibrium point  $E$  depends only on  $\alpha$ 's and  $K$ 's. For some cases with two possible final outcomes

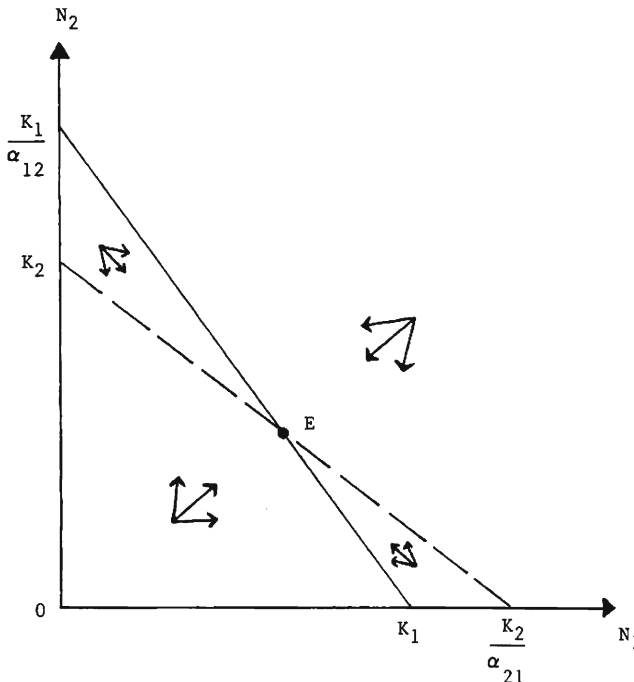


Fig. 3 Final equilibrium ( $E$ ) determined by  $\alpha$ 's and  $K$ 's, not by  $r$ 's or  $b$ 's

(extinction of either species), the initial population sizes determine which species win but this is still independent of the  $r$ 's.

The above remarkable results of the L-V model have important implications for our purpose here. Since the outcome is independent of the  $r$ 's (and hence  $b$ 's), the choice of  $b$ 's to maximize welfare (instead of say growth as might be favoured by natural selection) does not affect the equilibrium population sizes but increases welfare, possibly from a negative to a positive figure. Moreover, since the choice of  $b_i$  affects only  $r_i$  but not  $\alpha$ 's and  $K$ 's (within the L-V model; see below for complications), the choice of  $b_i$  does not affect the equilibrium outcome in terms of population sizes and does not affect the welfare of the other species *in the equilibrium outcome*. Thus, the choice of  $b_1$  to maximize  $W_1$  and the choice of  $b_2$  to maximize  $W_2$  (both at the equilibrium outcome) gives the solution to the maximization of  $W_1 + W_2$  at the equilibrium outcome.

If the initial position is not at the equilibrium point, the choice of  $b$  maximizing welfare at the equilibrium outcome need not necessarily maximize the present value of (possibly discounted) welfare through time. In particular, welfare over the adjustment path towards equilibrium needs not be maximized. Analysis of adjustment paths is very complicated. However, for any non-trivial intrinsic growth rate, since the population size converges rather quickly to the equilibrium figure, the divergence in welfare between the two is relatively small, for any relatively small discount factor. Since the discount factor is purely an uncertainty discount, not the economic rate of interest, it should be rather small unless the populations concerned are facing very high probability of destruction in the near future.

The L-V competition model for two species can easily be generalized to any number of species. (However, with more than two species, the total effect of one species on another may differ not only quantitatively but also qualitatively from the direct effect, even if all direct effects are of the same sign. See Lawlor 1979; Levine 1976; Tilman 1987.) Instead of (17), we have, for all  $i$ ,

$$\frac{\dot{N}_i}{N_i} = r_i \left( 1 - \frac{N_i}{K_i} - \frac{\sum_{j \neq i} \alpha_{ij} N_j}{K_i} \right). \quad (23)$$

From this, the condition for equilibrium ( $\dot{N}_i = 0$  for all  $i$ ) is, for each  $i$ ,

$$N_i = K_i - \sum_{j \neq i} \alpha_{ij} N_j. \quad (24)$$

Solving the equation in (20) by Cramer's Rule, we have, for each  $i$ ,

$$N_i = \frac{D^i}{D} \quad (25)$$

where  $D$  is the determinant of the relevant matrix and  $D^i$  is the determinant of the same matrix after replacing its  $i$ th-column by the column vector  $(K_1, \dots, K_m)$ . The solution for equilibrium values of the  $N$ 's in (25) again depends only on the  $\alpha$ 's and  $K$ 's, but not on the  $r$ 's.

In the generalized model for  $m$  species, not all the  $\alpha$ 's need assume positive values. Thus, non-competition relationships between species, such as symbiosis, may be modelled by negative  $\alpha$ 's. Moreover, the model can be further generalized

while preserving the independence of equilibrium  $N$ 's from the  $r$ 's. Hence we have, instead of (23),

$$\frac{\dot{N}_i}{N_i} = r_i F_i (\alpha's, K's, N's) \quad (26)$$

for all  $i$ , where  $F_i$  is a function. Equilibrium then requires, for each  $i$ ,

$$F_i (\alpha's, K's, N's) = 0. \quad (27)$$

The  $m$  equations in (27) then give the  $m$  equilibrium values of  $N$ 's as functions only of the  $\alpha$ 's and  $K$ 's.

The analysis above may be briefly summarized. The number of offspring of a species that maximizes fitness may lead to suffering and is different from the number that maximizes welfare (average or total). In the L-V model of competing species and its generalizations, the choice of different birthrates does not affect the population sizes at equilibrium. Welfare could be much higher at lower birthrates without even reducing numbers (at equilibrium).

Of course, even (26) is not a perfectly general model of population dynamics. One can construct hypothetical counter-examples to the independence of equilibrium  $N$ 's from  $r$ 's. One can also point out aspects of the real-world population dynamics that tend to point to the possible dependence. This means that the choice of optimal  $b$ 's may significantly change the values of the  $N$ 's. But this does *not* mean that the existing  $b$ 's or the  $b$ 's that maximize growth also maximize welfare. The contrast between growth and welfare maximization still applies, in general, to the complicated real world, but also in a complicated way.

## 5 Conclusion

Being an initial attempt at a welfare calculus of species, this paper is purposefully confined to very simplified models, ignoring many relevant issues such as extinction and viable population, heterogeneous and variable environments, etc. (On these issues, see, e.g., Abrams 1991; Bernstein et al. 1988; Chesson 1985; Cohen and Levin 1991; Darwin and Green 1996; Demetrius 1992; Derrick and Metzgar 1991; Grover 1992; McLaughlin and Roughgarden 1991; Palmqvist and Lundberg 1998; Ripa and Lundberg 2000; Soule 1987; Sutherland and Norris 2002; Tuljapurkar 1980; Waage et al. 1985.) The consideration of these issues may mean that we have to be very cautious in actually undertaking any action, yet the experience of Puckapunyal demands some action. While our discussion above may give some support to the culling of kangaroos or other animals in certain circumstances, a more preventive measure may be superior to the resort to culling. We may not be able to do much in practice yet. (However, see Ng 1995 for some analysis.) Nevertheless, conceptual consideration of the problem is urgently required. While the generalization of our analysis to, say, a sexually reproducing population may be straightforward; the consideration of other complications may need considerable ingenuity. A more general model might also take into account the dependence of not just the number of individuals but also the average welfare level of a species on other species. It would be interesting to see whether some new results may be obtainable from such generalizations, but it is definitely beyond the scope of the present paper.

## References

- Abrams PA (1991) The effects of interacting species on predator-prey coevolution. *Theor Popul Biol* 39:241–262
- Bernstein C, Kacelnik A, Krebs JR (1988) Individual decisions and the distribution of predators in a patchy environment. *J Anim Ecol* 57:1007–1026
- Blackorby C, Donaldson D (1984) Social criteria for evaluating population change. *J Public Econ* 25(1–2):13–34
- Blackorby C, Donaldson D (1992) Pigs and guinea pigs: a note on the ethics of animal exploitation. *Econ J* 102(415):1345–69
- Broome J (2001) Measuring the burden of disease by aggregating well-being. In: Murray C., Salomon J., Mathers C., Lopez A. (eds) *Summary measures of population health: concepts, ethics, measurement and applications*. World Health Organization, Geneva
- Chesson PL (1985) Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theor Popul Biol* 28:263–287
- Cohen D, Levin SA (1991) Dispersal in patchy environments: the effects of temporal and spatial structure. *Theor Popul Biol* 39:63–99
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Am Nat* 122:661–696
- Cressman R, Garay J (2003) Evolutionary stability in Lotka-Volterra systems. *J Theor Biol* 222:233–245
- Darwen PJ, Green DG (1996) Viability of populations in a landscape. *Ecol Model* 85(2–3):165–171
- Demetrius U (1992) Growth rate, population entropy, and evolutionary dynamics. *Theor Popul Biol* 41:208–236
- Derrick W, Metzgar L (1991) Dynamics of Lotka-Volterra systems with exploitation. *J Theor Biol* 153:455–468
- Edmunds J, Cushing JM, Costantino RF, Henson SM, Dennis B, Desharnais RA (2003) Park's Tribolium competition experiments: a non-equilibrium species coexistence hypothesis. *J Anim Ecol* 72:703–712
- Gillespie JH (1998) *Population genetics: a concise guide*. The Johns Hopkins University Press, Baltimore, MD
- Gordon CE (2000) The coexistence of species. *Rev Chil Hist Nat* 73(1):175–198
- Grover JP (1992) Constant- and variable-yield models of population growth: responses to environmental variability and implications for competition. *J Theor Biol* 158:409–428
- Harrod R (1948) *Towards a dynamic economics*. Macmillan, London
- Hicks J (1940) The valuation of social income. *Economica* 7:104–24
- Huang X, Zu Y (2001) The LES population model: essentials and relationship to the Lotka-Volterra model. *Ecol Model* 143(3):215–225
- Kahneman D, Wakker PP, Sarin R (1997) Back to Bentham? Explorations of experienced utility. *Q J Econ* 112(2):375–405
- Lawlor LR (1979) Direct and indirect effects of n-species competition. *Oecologia (Berl.)* 43:355–364
- Levine SH (1976) Competitive interactions in ecosystems. *Am Nat* 110:903–910
- McLaughlin JF, Roughgarden J (1991) Pattern and stability in predator-prey communities: how diffusion in spatially variable environments affects the Lotka-volterra model. *Theor Popul Biol* 40:148–172
- Ng Y-K (1983) Some broader issues in social welfare. In: PK Pattanaik, Salles M (eds.) *Social choice and welfare*. North Holland, Amsterdam
- Ng Y-K (1984) Expected subjective utility: is the Neumann–Morgenstern utility the same as the neoclassical's? *Soc Choice Welf* 1:177–186
- Ng Y-K (1986) On the welfare economics of population control. *Popul Develop Rev* 12:247–266
- Ng Y-K (1989) What should we do about future generations? Impossibility of Parfit's Theory X. *Econ Philos* 5:235–253
- Ng Y-K (1991) Should we be very cautious or extremely cautious on measures that may involve our destruction? On the finiteness of our expected welfare. *Soc Choice Welf* 8:79–88
- Ng Y-K (1995) Towards welfare biology: evolutionary economics of animal consciousness and suffering. *Biol Philos* 10:255–285

- NG Y-K (2000a) Efficiency, equality, and public policy: with a case for higher public spending. Macmillan, Basingstoke, Hampshire
- Ng Y-K (2000b) From separability to unweighted sum: a case for utilitarianism. *Theory Decis* 49:299–312
- Palmqvist E, Lundberg P (1998) Population extinctions in correlated environments. *Oikos* 83(2):359–367
- Parfit D (1984) *Reasons and persons*. Cambridge University Press, Cambridge
- Pigou AC (1929) *The economics of welfare*. Macmillan, London
- Ramsey FP (1929) A mathematical theory of saving. *Econ J* 38:543–559
- Ripa J, Lundberg P (2000) The route to extinction in variable environments. *Oikos* 90(1):89–96
- Roughgarden J (1979) *Theory of Population Genetics and Evolutionary Ecology*. Macmillan, New York
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:583–601
- Schoener TW (1985) Some comments on Connell's and my reviews of field experiments on interspecific competition. *Am Nat* 125:730–740, 126:300–301
- Singer P (1975) *Animal liberation: a new ethics for our treatment of animals*. Random House, New York
- Singer P (2000) *Writings on an ethical life*. Ecco, New York
- Soule M (ed) (1987) *Viable populations*. Cambridge University Press, Cambridge, England
- Sutherland WJ, Norris K (2002) Behavioural models of population growth rates: implications for conservation and prediction. *Philos Trans R Soc Lond, B Biol Sci* 357:1273–1284
- Tilman D (1987) The importance of the mechanisms of interspecific competition. *Am Nat* 129:769–774
- Tuljapurkar SD (1980) Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor Popul Biol* 18:314–342
- Turchin P (2003) *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, NJ, Oxford
- Waage JK, Hassell MP, Godfray HCJ (1985) The dynamics of pest-parasitoid- insecticide interactions. *J Appl Ecol* 22:825–838
- Weizsäcker CC (1965) Existence of optimal programs of accumulation for an infinite time horizon. *Rev Econ Stud* 32:85–104