

Fertility partially drives the relative success of two introduced bovines (*Bubalus bubalis* and *Bos javanicus*) in the Australian tropics

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Abstract

Context. Some large herbivores introduced to Australia have achieved population densities so high as to cause considerable ecological damage. Intriguingly, others have been relatively less successful and have correspondingly perturbed their new environments less. An excellent example is two similar-sized bovine species that established feral populations in the Northern Territory of Australia in the mid-19th century. Asian swamp buffalo (*Bubalus bubalis*) rapidly colonised the tropical savannas, causing ecological degradation, especially on freshwater swamps. In contrast, banteng (*Bos javanicus*) are restricted to their point of introduction and have caused relatively negligible ecological damage. Understanding the reasons of this differential success is of theoretical and applied interest and contributes to managing large herbivore populations for *ex situ* conservation and feral-animal control.

Aims. To compare the population structure of buffalo and banteng on the basis of shot samples, so as to construct life tables for four contemporary (low-density) buffalo populations, and collated data from previous work from three historical (high-density) buffalo populations and one banteng population (the only extant *ex situ* population in existence). Further, to provide a validation of age estimation with and without informed priors in a Bayesian model comparing horn length and ages estimated from tooth *cementum annuli*. Finally, to interpret our results in the context of relative invasion potential of the two bovid species.

Key Results. For both species, survival of juveniles was the most important demographic component influencing deterministic population growth. However, buffalo have the demographic capacity to recover swiftly after control because of high survival and fertility rates across a range of population densities. Fertility of buffalo was historically greater than that of banteng, and buffalo fertility increased as their populations were reduced.

Conclusions. These findings highlight how subtle differences in demographic rates and feeding ecology can influence the success (high population growth and range expansion) of large herbivores, knowledge which is increasingly important for managing invasive species effectively.

Implications. We show that that individual life-history traits and demographic performance, especially fertility, play an important role in determining the spread of invasive bovids in a novel environment.

Additional keywords: age, banteng, fertility, herbivores, invasive species, life table, survival, swamp buffalo, wildlife management.

Introduction

Perturbations to ecosystems caused by introduced non-indigenous animals are a major driver of biotic change around the world (Clavero and García-Berthou 2005; Ricciardi 2007; Salo *et al.* 2007), with Australia's biodiversity suffering particularly from introduced species (Lunney 2001; James 2003; Tait *et al.* 2005; Reddiex and Forsyth 2006; Reddiex *et al.* 2006; Bradshaw *et al.* 2007a; Johnson *et al.* 2007). Two

such species are the Asian swamp buffalo (*Bubalus bubalis*) and the banteng (*Bos javanicus*). The now-abundant Australian populations established from small founder populations in the 19th century when they were introduced as domestic animals and quickly released into the wild. Currently, the Australian banteng population is estimated to be ~5000–7000 (Bradshaw *et al.* 2007b), with the total population of buffalo ~80 000–150 000 (Bradshaw *et al.* 2007a; Albrecht *et al.* 2009). Buffalo have had

large ecological impacts in some freshwater swamp forests (Bowman *et al.* 2010a) and influence savanna dynamics via their effect on fuel loads and fire regimes (Lehmann *et al.* 2009). However, the ecological impacts of banteng remain poorly studied and it is difficult to quantify the role they play in altering landscapes over the long-term (Bowman and Panton 1994).

The sharply contrasting relative success (Fig. 1) and ecological effects of these closely related species are biogeographically puzzling and highlight the broader controversy that surrounds identifying those life-history and ecological attributes that determine extinction or invasion propensity (Forsyth *et al.* 2004; Lockwood *et al.* 2005; Jeschke and Strayer 2006; Croci *et al.* 2007; Bradshaw *et al.* 2008; Kanarek and Webb 2010). Here, we study the life history of two large, introduced (at the same time and with approximately similar founder size and frequency) vertebrates of similar size and in the same family (Bovidae) to discover what has driven one, namely buffalo, to be highly successful (abundant and widespread population), and the other, banteng, less so (substantially smaller population restricted to its introduction site). Examining these mechanisms can enhance our understanding of patterns of invasiveness and provide insight into management strategies for controlling further establishment of introduced populations (Forsyth *et al.* 2004; Bradshaw *et al.* 2008; Kanarek and Webb 2010).

Central to any insight to the mechanics driving the likelihood of a species establishing itself in a new environment, either as an invasive species or as part of a deliberate introduction for conservation management, is an understating of the basic demographics of the species in question, the number of animals introduced and the number of introduction sites (Forsyth and Duncan 2001; Forsyth *et al.* 2004). The introduction of buffalo and banteng to Australia offers an excellent opportunity to test hypotheses about introduction dynamics because both species (1) had similar establishment probabilities (Forsyth and Duncan 2001), given introduction numbers of 80 and 20, respectively, and similar introduction sites, (2) are approximately the same size (female adult mass is 350 and 300 kg, respectively) (Forsyth *et al.* 2004), (3) occupy native habitats similar to the monsoon tropics into which they were introduced and (4) were widespread in their native ranges. Because many of the principal drivers of introduction success (Forsyth and Duncan 2001; Forsyth *et al.* 2004; Forsyth and Caley 2006) were similar, we must investigate other aspects of their biology to determine which mechanisms have driven their relative success in Australia.

History of buffalo and banteng introductions

The first swamp buffalo introduced to Australia was a shipment of 16 animals onto Melville Island (Fig. 1) to the north of Darwin

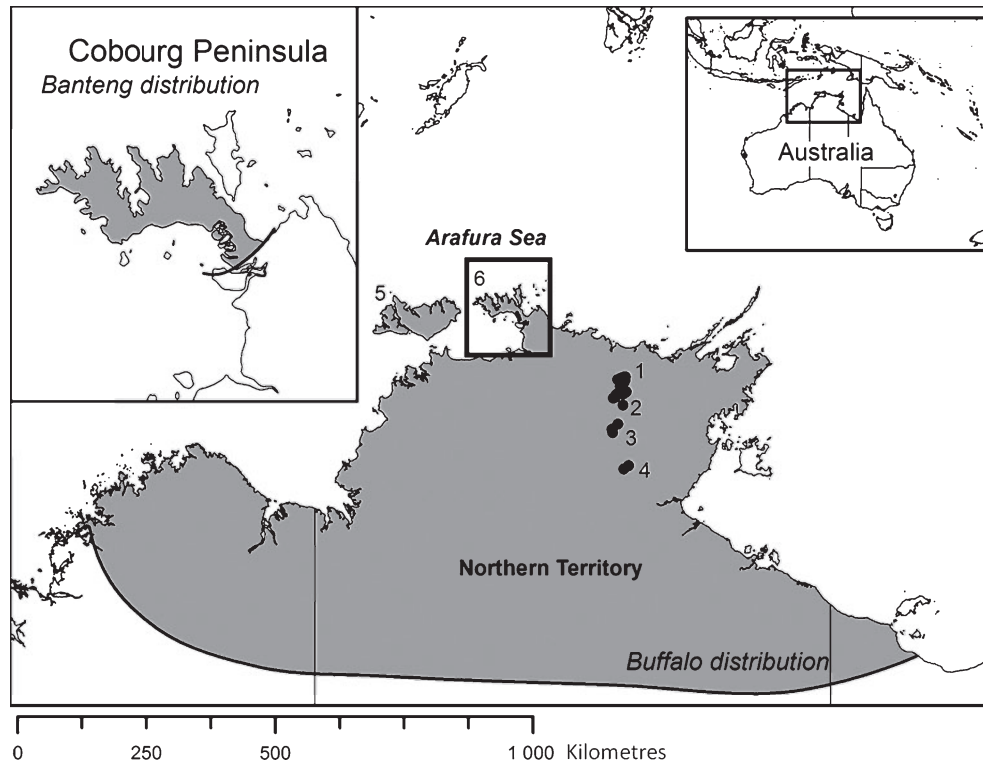


Fig. 1. The distribution of introduced swamp buffalo (*Bubalus bubalis*) and banteng (*Bos javanicus*) in northern Australia. Both buffalo and banteng were introduced to the Cobourg Peninsula in the 1820s, but only buffalo have spread widely across northern Australia. Shown are the four locations (Kolorbidahdah (1), Wilton River (2), Bulman (3) and Wongalara (4)) at which swamp buffalo were sampled to construct the contemporary life tables. Also shown are the two initial introduction sites in the 1820s, namely Melville Island (5) in 1826 and the Cobourg Peninsula (6) in 1827. Solid circles show the locations at which buffalo were sampled.

in 1826 (Letts 1962). Buffalo were first introduced to mainland Australia on the Cobourg Peninsula a year later in 1827 from Kupang (now West Timor, Indonesia). Another 18 individual buffalo were obtained from Kisar Island (north-east of modern Timor-Leste) and introduced to Victoria Settlement in Port Essington on the Cobourg Peninsula (Letts 1962). Five years later, in 1843, another 49 individual buffalo were introduced to Port Essington from Raffles Bay (Letts 1962). When the Port Essington settlement was abandoned in 1849, all the buffalo breeding stock was released, and buffalo spread rapidly throughout the Northern Territory, forming vast herds across north-central Australia. Indeed, so rapidly did the population grow that by the 1880s, there was a lucrative trade in wild-shot buffalo skins (an average of 4000 skins were collected annually between 1880 and 1911) (Letts 1964; Tulloch 1969). Over the next 65 years, numbers and distribution increased to an estimated 350 000 in the 1960s and 1970s, with densities $>25 \text{ km}^{-2}$ in 'prime' habitat (Bayliss and Yeomans 1989; Freeland and Boulton 1990). However, the buffalo population was severely reduced during the 1980s and 1990s in parts of its range under the Brucellosis–Tuberculosis Eradication Campaign (BTEC) (Radunz 2006). Although largely successful in eradicating buffalo from pastoral lands in the short term, there was no ongoing broad-scale management of numbers and the present-day population of free-ranging swamp buffalo has recovered to former densities in some areas (despite sporadic and limited aerial culls and safari hunting for trophy males) (Bradshaw *et al.* 2007a). Such observations underscore the invasive capacity of swamp buffalo and suggest this is driven by a high intrinsic capacity to increase in uncontrolled populations.

In contrast, the smaller founder population ($n=20$) of banteng (*Bos javanicus*) was introduced to Australia in the 1820s (Bradshaw *et al.* 2007b); however, the species did not spread widely across northern Australia and, currently, between 5000 and 7000 animals (Bradshaw *et al.* 2007b) remain close to the introduction site on the Cobourg Peninsula (Bowman *et al.* 2010b). It has been proposed that the banteng's restricted habitat use and specialised browser diet is largely responsible for limiting the invasive capacity of the species (Bowman *et al.* 2010b), and that this constrains population growth (Choquenot 1993) and dispersal capability (Bowman *et al.* 2010b). There is little evidence of environmental impacts from banteng beyond browse lines on palatable trees, and trampling vegetation on

trails and resting areas (Bowman and Panton 1994). Indeed Cobourg remains a stronghold of some mammals undergoing rapid range contractions (Woinarski *et al.* 1999, 2010).

Objectives and study design

Here, we provide the first empirical estimates of basic life-history rates such as age-specific survival and fertility rates of swamp buffalo in Australia, and contrast these with the measured vital rates of banteng (Choquenot 1993; Bradshaw and Brook 2007). We expect *a priori* to observe high age-specific survival and fertility rates in buffalo, but relatively lower values for the more range-restricted banteng. We studied four contemporary buffalo populations and collated published data for three historical buffalo populations (Tulloch and Grassia 1981; Purdie 1982; Boulton and Freeland 1991). These data provide an important point of comparison with the four contemporary datasets in terms of buffalo population structure when densities were relatively high and current populations at lower density. The banteng vital rates with which we contrast the buffalo data were collected previously and published as part of a study on the life history and growth of banteng on the Cobourg Peninsula, Arnhem Land (Choquenot 1993). Our dataset also permits the comparison of population dynamics arising in harvested and unharvested populations. Specifically, we (1) construct age-specific life tables to (i) identify which demographic components most influence population growth rate (λ), and (ii) provide demographic descriptions of populations with contrasting densities, (2) provide a validation of age estimation with and without informed priors in a Bayesian model comparing horn length and ages estimated from tooth *cementum annuli*, and (3) interpret our results in the context of relative invasion potential of buffalo and banteng in Australia.

Materials and methods

Sampled data

We collected cross-sectional population data (Caughley 1977) based on shot samples and tooth examinations to age individuals from four distinct populations of buffalo exposed to differing rates of harvest from June 2006 to July 2007, and from a single population of banteng in Arnhem Land, northern Australia, shot in the early 1990s (Fig. 1, Table 1). In addition to the four contemporary buffalo datasets, we collated three historical

Table 1. Population names, harvest history and samples sizes of the four contemporary and three historic buffalo (*Bubalus bubalis*) populations and the single banteng (*Bos javanicus*) population used in the study

Species and population	<i>n</i>	Sample method	Sample date	Harvest history	Reference
<i>Bubalus bubalis</i>					
Kolorbidahdah	200	Cull	October 2006	Subsistence	This study
Wilton River	304	Cull	October 2007	Occasional	This study
Bulman	520	Muster	October 2007	Annual	This study
Wongalara	225	Muster	October 2008	None	This study
Purdie	219	Cull	1980–81	Unknown	Purdie (1982)
Boulton	88	Cull	1968	Unknown	Boulton and Freeland (1991)
Tulloch	1229	Cull	1968	Unknown	Tulloch and Grassia (1981)
<i>Bos javanicus</i>					
Cobourg	125	Cull	1992	Occasional	Choquenot (1993)

buffalo datasets (Table 1) collected before a broad-scale eradication program targeting buffalo and cattle in the 1980s (Tulloch and Grassia 1981; Purdie 1982; Boulton and Freeland 1991). These data provide an important point of comparison with the four contemporary buffalo datasets in terms of describing population structure when densities were relatively high compared with current populations. From these eight age–frequency datasets, we calculated eight separate, site-specific life tables. Calculating life tables by using this method relies on either the population being stable or knowledge of the rate at which it is changing (Caughley 1970; Caughley 1977), data that are not always readily available for wild populations in remote areas such as the buffalo and banteng populations sampled here. Nonetheless, some population-trend information is available for two (Kolorbidahdah and Wilton River) of our four contemporary populations, suggesting that these populations are currently stable (Koenig *et al.* 2003; Gorman *et al.* 2007). We have no evidence to conclude that either the Bulman or Wongalara populations are any different. Nonetheless, to investigate the effect different rates of population change might have on our observations, we recalculated survival on the basis of three different finite population growth rates, namely $\lambda = 0.9, 1.0$ and 1.1 .

The accuracy of this method is contingent on an unbiased sampling protocol; given that entire family groups were culled, i.e. eradication of all individuals from small patches of occupied habitat and the small ranges that buffalo occupy (Tulloch 1978), it is reasonable to assume that sampling was random. Moreover, not only were our samples of entire groups, they also occurred at the same time of year (September–October), so that any biases that might have been introduced due to shifts in social structure of the groups (Tulloch 1978; Tulloch and Grassia 1981) were negated. Consequently, we are confident that our demographic rate estimates from life tables are appropriate because (1) the samples represent an unbiased representation of the living age distribution, given that all animals in a group were sampled, (2) there is little evidence to suggest that mortality or fertility has changed appreciably, and (3) population growth rates appear low (close to zero) when samples were collected, although we do acknowledge that population growth might have been high in the intervening periods. Although we are confident that our contemporary datasets are from random culls, we concede that the historic samples might not necessarily be random. However, given that the historic samples were derived from wild, free-ranging individuals where the aim was to remove all animals from a particular area, it is reasonable to assume randomness, given there was no incentive to be selective during culls (Radunz 2006).

Life tables are used to characterise the survival properties of cohorts and provide important insights into a population's probability of long-term persistence under various ecological and management scenarios (Caughley 1977; Sinclair *et al.* 2006). Accurate ageing is at the core of demographic analyses (Caughley 1977; Sinclair *et al.* 2006). We estimated the age of each sampled animal using the following two techniques: (1) comparing established tooth-eruption and -wear patterns (Low and McTaggart Cowan 1963; Tulloch 1969; Moran 1992) and (2) counting *cementum annuli*; *cementum* layers are deposited continuously on the external root surface of teeth (Fancy 1980). However, the latter technique relies on a strong environmental seasonality, such as that which occurs in the

northern Australian monsoon tropics (Zhang 2009), and is therefore an appropriate ageing method that works well for large ungulates in northern Australia (Choquenot 1993). We counted the *cementum annuli* in the primary incisor (I_1) for older animals (Low and McTaggart Cowan 1963; Tulloch 1969), and because I_1 erupts at the age of three in swamp buffalo (McCool *et al.* 1990; Moran 1992), we added 3 years to each estimate of the total number of *cementum* layer numbers to estimate the age in whole years. For animals in which the permanent I_1 had not erupted, we estimated the age by using tooth-eruption patterns (Tulloch 1969).

We corroborated the derived ages by comparing our estimates (*cementum annuli* and eruption and wear patterns) with those from sex-specific algorithms relating buffalo horn length (H) and age (A) (McCool *et al.* 1990):

$$A = \log_e \frac{(1 - H)/a}{b/c} \quad (1)$$

where $a = 90.235$ and 88.846 , $b = 1.008$ and 0.991 and $c = -0.219$ and -0.183 for males and females, respectively. We did this to provide an independent estimate of age to verify the ages we determined from examination of the *cementum annuli*. These published data were also used as prior information in a Bayesian regression analysis of the age–horn length relationship, using WinBUGS v1.4.3 (www.mrc-bsu.cam.ac.uk/bugs). The prior was specified as a Gaussian error distribution (with a mean and s.d.) (McCool *et al.* 1990), and inference was based on 100 000 posterior samples after a 10 000 sample burn-in.

Life tables

Once the ages were estimated, we constructed an age–frequency distribution with corresponding age-specific fertility rates for the female component of the population and constructed life tables (Caughley 1966, 1977; Sinclair *et al.* 2006), specifically by using Caughley's 'Method 6' (Caughley 1977). Method 6 applies to a population with a stable age distribution, known rates of increase and an annual birth pulse so that distinct cohorts are recognisable, such as those observed for buffalo and banteng in Australia (Tulloch and Grassia 1981; Choquenot 1993). Here, the proportion of individuals surviving at the start of age x (l_x) is

$$l_x = n_x e^{rx} / n_0, \quad (2)$$

where n_x = the number observed in age class x to $x + 1$ and n_0 = the number of births estimated from the fertility data. We determined age-specific female fertility (m_x) by examining for evidence of lactation and pregnancy in females.

This information summarised the age-specific survival (l_x), mortality (d_x) and fertility (m_x) up to the maximum observed age of 17 years for buffalo. Age-frequency distributions collected from wild animals often do not decrease at constant rates or smoothly (since a single cohort is not being followed), which can lead to negative d_x estimates that are biologically implausible (Caughley 1966; Caughley 1977). Accordingly, we smoothed the observed age-frequency data (Caughley 1966) into an adjusted age-frequency (F_x). The most common smoothing algorithm, and the one we applied, is a log-polynomial regression which takes the general form $\log(f_x) = a + bx + c^2x + d^3x \dots$. Given that it is rare for the log-polynomial fitted to an age distribution from age 1 to

extend beyond the quadratic term (x^2) (Caughley 1966, 1977), we smoothed (F_x) our raw frequencies (f_x) using the quadratic form of the log-polynomial.

We assessed average differences in the smoothed age-frequency function between the contemporary and historical populations (4 and 3 populations combined, respectively) to test the hypothesis that smoothing function was equal between periods. We used Akaike’s information criterion corrected for small samples (AIC_c) (Burnham and Anderson 2002) to rank four candidate polynomial models with and without a two-level period factor (contemporary and historical populations).

To assess the relative contribution to population growth of each age-specific rate, we calculated deterministic elasticities (proportional sensitivities) (Heppell *et al.* 2000; Caswell 2001) using the program PopTools (Hood 2010). There are two ways of describing the proportional impact that age-specific survival and fertility have on λ , namely by (1) calculating the parameter sensitivity and comparing them directly, or (2) calculating parameter elasticities and comparing them (Caswell 2001; Caswell and Takada 2004). Survival (between 0 and 1) and fertility (0 and >1) are measured on different scales; it is therefore preferable to use the dimensionless elasticity values (Caswell 2001; Caswell and Takada 2004). This is especially relevant for buffalo where annual fertility rates in captivity generally vary from 0 to 0.5 (i.e. one female offspring per mother per year) (Fischer 1966; Fisher and Bodhipakasha

1992). To simplify the interpretation of the elasticity results, we grouped age-specific results into juvenile (non-breeders) and adult (breeders) categories, which necessarily varies between populations according to the age of primiparity that was not the same for all populations (McMahon *et al.* 2005; Owen-Smith and Mills 2006).

Results

Buffalo age estimates

From the measurements of horn length and estimates of age we present gender-specific algorithms describing the contemporary relationship between horn length (H) and age (A) from Eqn 1 (Table 2). The Bayesian modelling with informative priors yielded posterior parameter estimates that were similar to the maximum likelihood estimates (Table 2). The prior information (McCool *et al.* 1990) was consistent with the new sample data (Fig. 2) and narrowed the credibility intervals (Table 2). Moreover, these data show that male buffalo horns grow faster and longer than female buffalo horns and that horn length can be a useful field tool to age buffalo (Fig. 3).

Buffalo life tables

Estimated from age frequency (f_x) distributions, annual survival rates for buffalo varied among sites (Table A1, available as an Accessory Publication on the web), with survival of younger

Table 2. A comparative summary of the sex-specific parameters derived from gender-specific algorithms (Eqn 1), with or without priors, relating buffalo horn length (H) and age (A) (McCool *et al.* 1990)

a = asymptotic value of horn length, b = constant growth coefficient, c = estimated intrinsic proportional horn length growth rate; Bayesian 95% credibility interval (CI) is given in parentheses. Values are means \pm s.d.

Parameter	Male without priors	Male with priors	Female without priors	Female with priors
a	0.709 \pm 0.094 (0.557 to 0.936)	0.851 \pm 0.155 (0.636 to 1.244)	0.769 \pm 0.027 (0.720 to 0.826)	0.771 \pm 0.027 (0.722 to 0.828)
b	1.236 \pm 0.313 (0.732 to 1.908)	0.990 \pm 0.082 (0.834 to 1.154)	1.016 \pm 0.023 (0.971 to 1.063)	1.014 \pm 0.023 (0.970 to 1.061)
c	-0.596 \pm 0.228 (-0.001 to -0.193)	-0.306 \pm 0.109 (-0.115 to -0.539)	-0.223 \pm 0.019 (-0.188 to -0.262)	-0.222 \pm 0.019 (-0.187 to -0.259)

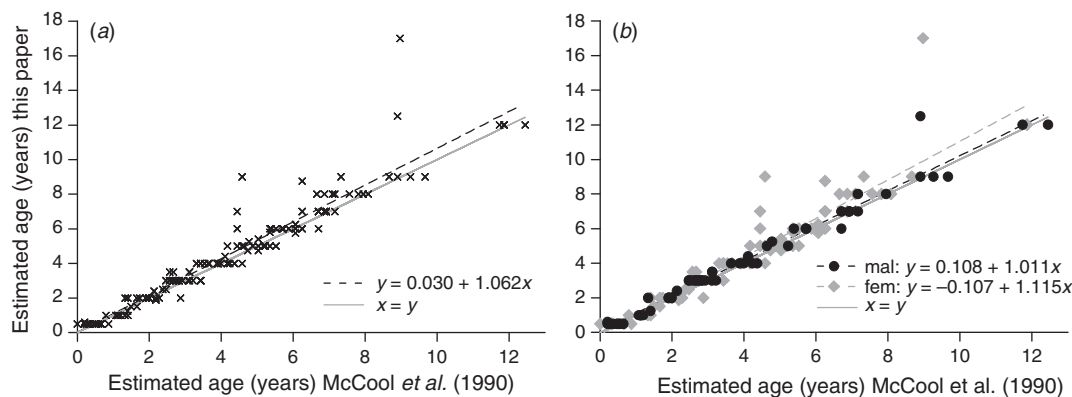


Fig. 2. The relationship between (a) age estimates for feral swamp buffalo in northern Australia determined by counting *cementum annuli* from sectioned permanent lower incisor 1 (I_1) (the present paper) and those estimated from horn lengths (McCool *et al.* 1990). The dotted black line represents the line of best fit ($y = 0.030 + 1.062x$, $R^2 = 0.917$) and the solid grey line represents $y = x$. (b) The gender-specific relationships as above for male and female buffalo separately.

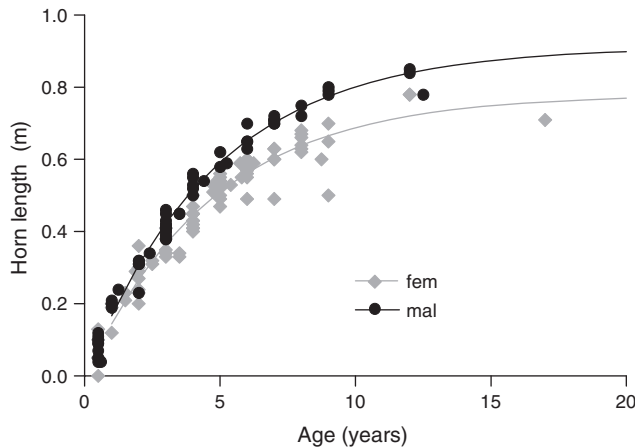


Fig. 3. The non-linear relationship between horn length (m) and age (years) of female and male swamp buffalo.

animals ranging from 0.47 to 0.82, whereas adult survival varied from 0.66 to 1.00. However, there were no clear differences in survival estimates at differing animal densities (Fig. 4), which is in contrast to our estimates of fertility. Indeed, the model combining the contemporary and historical smoothed age-frequency functions had more support than the models differentiating them (Table 3). Age-specific fertility (m_x) was lower (0.37–0.43) in the three historic datasets (i.e. during high buffalo density) than in the four contemporary (low-density) populations (0.34–0.60) (Fig. 5b). We found that survival curves for all the contemporary populations tended to fall near or outside of the mean survival estimates calculated for three rates of change ($\lambda = 0.9, 1.0$ and 1.1), providing some evidence to suggest that currently, the sampled buffalo populations are decreasing at 2–7.5% year⁻¹, compared with banteng, which is estimated to be increasing at 2.4% year⁻¹ (rates of change calculated after submitting the smoothed survival estimates to a life-table analysis such that $\lambda = R_0^{(1/G)}$, where R_0 = net reproductive rate per generation and G = mean generation time) (Caswell 2001). Given that data for the historic buffalo populations are subject to several assumptions, including general estimates of reproductive output, we cannot calculate defensible, representative estimates of the actual population change for these populations. We do, therefore, acknowledge that if the population is decreasing at a low rate, these estimated survival rates might be downwardly biased.

There was high variability in juvenile survival among sites, with elasticity results indicating that juvenile and adult survival had the greatest relative influence on population growth, followed by fertility (Fig. 5). In the annually harvested population at Bulman, juvenile survival appeared to make a relatively higher proportional contribution (0.52) to population growth than in the other populations (0.43–0.49), with adult fertility also contributing proportionally more to population change (0.17) than in the other six populations (0.12–0.13) where juvenile animals are not harvested as intensively.

Most females of breeding age were reproductively active (Kolorbidahdah = 0.89, Bulman = 0.83, Wilton River = 0.77, Wongalara = 0.83). In each of the four populations, even those

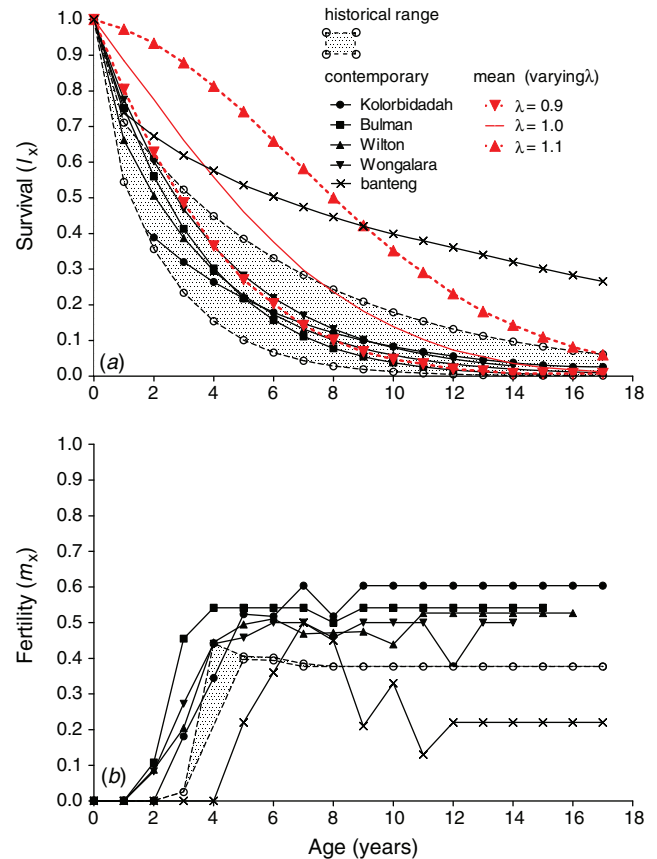


Fig. 4. (a) Age-specific survival (l_x) for seven populations, including three historic populations (shaded area and open symbols) and four contemporary populations (solid symbols) of feral swamp buffalo and a banteng populations (\times) in northern Australia. Also shown are survival estimates (mean of the four contemporary populations) under three different assumed rates of population growth, namely $\lambda = 0.9, 1.0$ and 1.1 , respectively. (b) Age-specific fertility (m_x) for the same eight populations.

Table 3. Four candidate models testing the relative support for the quadratic polynomial relationship between age (A) and the frequency of females in each yearly age class (f_x), including or not the two-level contemporary and historical period (per) factor

The hypothesis is that there is no difference in the quadratic frequency–age relationship between periods, a conclusion supported by the highest information-theoretic weight ($wAIC_c$, where AIC_c is Akaike’s information criterion corrected for small samples) for the model excluding the per factor. Also shown is the number of model parameters (k), maximum log-likelihood (LL), AIC_c and the difference between the AIC_c for the current and the top-ranked model (ΔAIC_c)

Model	k	LL	AIC_c	ΔAIC_c	$wAIC_c$
$f_x \sim A + A^2$	4	-39.342	87.974	0.000	0.5656
$f_x \sim per + A + A^2$	5	-38.971	89.942	1.969	0.2114
$f_x \sim per \times A + A^2$	6	-38.088	91.073	3.010	0.1201
$f_x \sim per \times A + per \times A^2$	7	-36.691	91.381	3.408	0.1029

females in the oldest age classes sampled (17 years) were observed with calves (Table A1). Age at primiparity was one year earlier in the commercially harvested Bulman

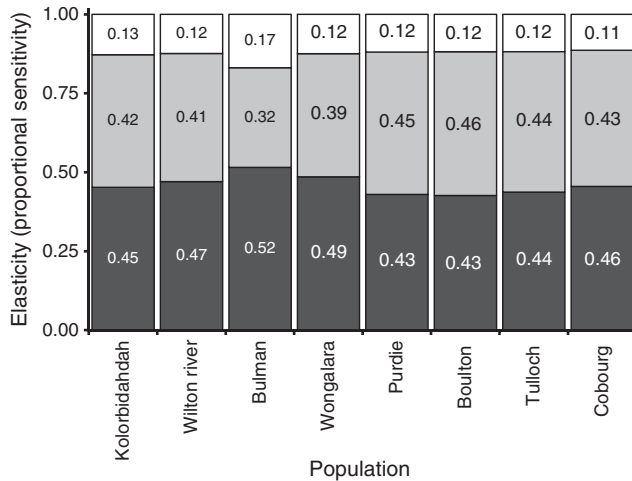


Fig. 5. The proportional sensitivities (elasticities) of buffalo and banteng vital rates (juvenile survival (black), adult survival (grey) and adult fertility (white)) on population growth from four contemporary north Australian buffalo populations at relatively low densities (Kolorbidahdah, Bulman, Wilton River and Wongalara), three historical populations at relatively high densities (Tulloch, Boulton and Purdie) and the banteng population on the Cobourg Peninsula.

population compared with the Kolorbidahdah and Wilton River populations (Table A1). There was some evidence for departure from equal neonate sex ratios (M : F) on the basis of a binomial randomisation test (100 000 iterations testing the null hypothesis M : F = 1 : 1) for the Kolorbidahdah and Wongalara populations (M : F = 1.73 : 1, $P_{\text{random}} = 0.10$; and M : F = 2 : 1, $P_{\text{random}} = 0.09$, respectively), but no evidence for such a sex bias in either the Wilton River (M : F = 1.11 : 1, $P_{\text{random}} = 0.39$) or Bulman (M : F = 1.18 : 1, $P_{\text{random}} = 0.25$) populations.

Banteng life tables

The vital rates observed for banteng differed markedly from those reported for buffalo, in that survival rate was higher in banteng whereas fertility rate was lower (Fig. 4a, b). Adult female banteng survival rate (l_x) was substantially higher (>0.92 on average) than that recorded for female buffalo (Fig. 4a), so that, cumulatively, there were many more adult females in the population. But this came at a cost such that adult age-specific fertility (m_x) was low (<0.30 on average) and in the first 6 months of life, mortality was high (>0.25). Juvenile and adult survival rates, as in all seven buffalo populations, contributed most to changes in population growth (Fig. 5).

Discussion

Despite being introduced to Australia at approximately the same time in the early 19th century, banteng are today restricted mainly to the Cobourg Peninsula, whereas buffalo have colonised large areas of northern Australia (Fig. 1). Buffalo have a generalist diet, and their success in northern Australia signals they are well adapted to the region's harsh monsoonal environment (Bowman *et al.* 2010b). We found that the current population of free-ranging swamp buffalo has high fertility rates (i.e. within

the range expected from captive buffalo), and high adult and juvenile survival rates. In contrast, the locally restricted banteng population on the Cobourg Peninsula has lower fertility possibly because the sampled population is near carrying capacity (Bradshaw and Brook 2007) and the population might be, by accident of the introduction site, restricted to relatively poor-quality forage (i.e. livestock fertility can vary according to pasture quality) (Richards *et al.* 1986). It is suspected that banteng are near carrying capacity because they have completely occupied available habitats within a relatively restricted area (McCool 1992; Choquenot 1993; Bowman *et al.* 2010b). Compared with swamp buffalo, banteng have a specialist diet (Bowman *et al.* 2010b), limited dispersal capacity (C. Bradshaw, unpubl. data) and had a lower propagule pressure at introduction (a single introduction of 20 animals compared with the 3 localised introductions of a total of 80 buffalo individuals) (Forsyth and Duncan 2001; Forsyth *et al.* 2004). However, it is unlikely that introduction dynamics alone can explain the differences in the current extent of buffalo and banteng because buffalo were also introduced at only one site on the mainland. It is thus a more parsimonious explanation that their generalist diet (Bowman *et al.* 2010b) and high fertility rates have played a role in the buffalo's successful invasion across northern Australia.

Buffalo fertility seems to respond more readily to changes in density than does survival, as might be anticipated for species with slower life histories. Average buffalo fertility was lower at high densities (before the 1980s' cull), which conforms to the sequence of changes in vital rates predicted for a population at or approaching carrying capacity (Eberhardt 2002). This sequence of changes in vital rates as a population increases towards its carrying capacity is as follows: (1) immature-animal survival decreases; (2) age at primiparity increases; (3) adult reproductive rate decreases; and (4) adult survival decreases (Eberhardt 2002). Although we do not have comparative data for banteng, we suspect that the fertility of this species follows a pattern similar to what has been shown for most ungulates examined (Gaillard *et al.* 2000). For buffalo, we found that the deterministic elasticity of adult survival was at least three times higher than that of either juvenile survival or fertility. The reduction of fertility at high densities partially contradicts the results of much previous work establishing that adult female fertility is relatively insensitive to shifts in density (reviewed in Gaillard *et al.* 2000). However, this density feedback mechanism is likely to be highly species-specific (Gaillard *et al.* 2000). Indeed, fertility responses to density should be more prominent in sedentary than migratory species (Skogland 1986). Further, there is evidence that domesticated ungulates returned to the wild are more likely to shift fertility in response to density than are their wild counterparts because artificial selection in domesticated species can result in higher average fertility (Grange *et al.* 2009).

We found that present-day buffalo fertility rates are higher than those observed at high buffalo densities recorded in the 1960s to 1990s. We also found some evidence that neonate sex ratios for two of our four recently sampled populations – Kolorbidahdah and Wongalara – were female-biased, likely driving an unbalanced adult sex ratio. A similar pattern has been observed in red deer (*Cervus elaphus*) where the number of females increased after the population was released from

regular culls that kept densities low (Coulson *et al.* 2004). This appears to be a predictable demographic response to a reduction in animal density. We thus expect that the sudden release from the mortality induced by the broad-scale eradication program lead to increases in buffalo abundance arising from improved reproductive rates, earlier onset of sexual maturity, increased survival of some population classes and faster recruitment (Coulson *et al.* 2004). Such rapid response in demographic rates allows even large-bodied mammals such as buffalo (post-culling) and banteng (post-introduction) to recover quickly from low densities.

We did not expect to find fertility to be the principal parameter explaining the difference in relative invasion success of both bovine species compared. We suspect that the lack of major predation on both species alters breeder-recruitment patterns (Tulloch 1970; Choquenot 1993), allowing populations to grow rapidly to carrying capacity, after which point, relative diet quality and foraging flexibility limit population growth. Previously (Choquenot 1990, 1993), a similar hypothesis was posed to explain the demographic characteristics of feral donkeys and banteng in northern Australia. Although buffalo and banteng are obviously able to survive and proliferate in north Australian savannas (Andrews 1972; Ford 1978, 1982; Moran 1986, 1992), both are vulnerable to extended periods of harsh conditions when forage quantity and quality can be severely reduced (Caughley and Sinclair 1994), which occurs there episodically (Freeland and Boulton 1990); banteng are especially susceptible to poor forage and low rainfall (Andrews 1972; Choquenot 1993). Progressing this issue demands more research targeted at understanding the nexus between diet, fertility, population densities and both adult and juvenile survival.

Survival estimates were consistently higher for banteng than for buffalo, which could arise in part from relatively different hunting pressures on the two species. However, this is an unlikely explanation because there is currently low-level hunting (safari and subsistence) for both buffalo (Petty *et al.* 2007) and banteng (deKoninck 2005; Brook *et al.* 2006; Bradshaw and Brook 2007).

The management and control of feral ungulates is often unsuccessful (Cruz *et al.* 2009), mainly because demographic data necessary to predict how populations respond to density reductions from culling are lacking; only with such information, can assessments of compensatory shifts in reproductive rates or mortality during control be made (Gogan *et al.* 2001; McMahon *et al.* 2010). However, our findings and those of others (see Grange *et al.* 2009, and references therein for a recent overview) describing the rapid shifts in vital rates facilitate and enhance the possibility of successful management. Successful management does not only rely on quantifying changes in vital rates (Grange *et al.* 2009), it depends perhaps even more importantly on the adoption of an experimental framework, which is generally lacking in most wildlife management research (Reddiex and Forsyth 2006).

We concede that successful management of feral animals does not depend solely on intimate knowledge of the target-species demography (Cruz *et al.* 2009), given that socio-political issues often dictate management efforts (Beever and Brussard 2000; Warburton and Norton 2009). However, resolving

socio-economic trade-offs ultimately demands high-quality population projections (Bradshaw and Brook 2007). For example, Bradshaw and Brook (2007) were able to explore the economic trade-offs associated with managing the feral banteng population, and Collier *et al.* (2011) determined that buffalo harvests provided lucrative employment benefits to indigenous Australians. Our work highlights the potential vulnerabilities in the demographics of the feral buffalo that might be exploited in crafting sustainable management options for this invasive species.

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