Is anti-predator behaviour in Tasmanian eastern quolls (*Dasyurus viverrinus*) effective against introduced predators?

Menna E. Jones, Georgina C. Smith and Susan M. Jones

School of Zoology, University of Tasmania, GPO Box 252-5, Hobart 7001, Australia

Abstract

Exotic predators, particularly red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), have been implicated in the declines and extinctions of many Australian mammals and a recent incursion of foxes into Tasmania has therefore caused great concern. We tested the behavioural responses of eastern quolls (*Dasyurus viverrinus*) to acoustic cues of native (masked owl (*Tyto novaehollandiae castanops*) and Tasmanian devil (*Sarcophilus laniarius*)) and non-native (fox and cat) predators and to non-predators (cow (*Bos taurus*) and control noise). Juvenile quolls treated fox vocalisations like those of cows (as measured by an increase in movement), in contrast to their responses (a decrease in movement) to sympatric predators. Cats are probably a lesser threat to eastern quolls than native predators or foxes, their impact probably being greatest on the juveniles. Juvenile quolls, but not adults, showed similar responses to cat vocalisations as they did to owls and devils. Adult quolls responded differently from juveniles to owls and devils, by increasing vigilance. This is consistent with the smaller body size, inexperience and the presumed greater vulnerability of juveniles to predation. The lack of appropriate anti-predator responses to foxes suggests that eastern quolls would be vulnerable to predation by foxes in Tasmania.

INTRODUCTION

The introduction by Europeans of evolutionarily novel predators (principally red foxes, *Vulpes vulpes*) and herbivores is one of the key processes that has probably driven the dramatic decline of native mammals across Australia (10% of marsupials are now extinct and more than half are threatened: Morton, 1990; Short & Smith, 1994; Caughley & Gunn, 1996; Maxwell, Burbidge & Morris, 1996). There is now strong evidence implicating predation by foxes in many of these declines (Short *et al.*, 1992; Dickman, 1996*a*). The island state of Tasmania has, however, harboured several species of Australian mammals that have either become extinct or declined dramatically on mainland Australia. The recent deliberate introduction of between 11 and 17 foxes to Tasmania in 1998 therefore poses a substantial threat to the one endemic Tasmanian mammal as well as to the four species now confined to Tasmania and the five species that are now rare on the mainland but still relatively abundant in Tasmania (see http://www.dpiwe.tas.gov.au/; Parks and Wildlife, Fox Sightings; Burbidge, 1999).

Evolutionarily novel predators may have devastating impacts because the potential prey species often lack appropriate responses to them (Coss, 1999). Since anti-predator behaviours are costly for some animals, the level of response may be finely tuned to the level of risk posed by sympatric predators (Brown, 1988; Brown, Laundré & Gurung, 1999). Knowledge of the presence or absence of a response is central to predicting the impact of a newly introduced, evolutionarily novel predator and in predicting whether predator control or anti-predator training are needed in conservation and reintroduction programs (see Curio, 1996; Clemmons & Buchholz, 1997; Caro, 1998; Gosling & Sutherland, 2000). The aim of this research was to test whether a mammal that is very vulnerable to fox predation displays anti-predator behaviours similar to those it displays towards native predators and cats (with which it has co-existed for 200 years).

Eastern quolls (*Dasyurus viverrinus*; Dasyuridae: Marsupialia) are a medium-sized (females–males = 0.7–1.5 kg) marsupial carnivore that live at low density across most of their range and are at risk of extinction (Maxwell *et al.*, 1996; IUCN, 2003; Cardillo & Bromham, 2001; Johnson, Delean & Balmford, 2002). Their mainland Australian range decreased dramatically between the late 1800s, (following the arrival of foxes in a local district) and the mid-1960s, when the last mainland population became extinct (for a review, see Jones *et al.*, 2003). By contrast, in Tasmania, eastern quolls have persisted over the last 200 years of European settlement despite the introduction of cats (Rolls, 1969). However, the predatory impact of cats on eastern quolls and the anti-predator strategies employed by eastern quolls remain unknown (Dickman, 1996*b*, *a*).

All correspondence to: Menna Jones.
E-mail: menna.jones@utas.edu.au

For eastern quolls, we consider acoustic detection of predators to be the more important of the three primary sensory modes (acoustic, olfactory and visual, in order of importance). Vocalisations are generally species-specific, providing the potential for prey to distinguish between different species of predators (Blumstein *et al.*, 2000). While predators usually hunt in silence, prey can use vocalisations directed at conspecifics or other predators to detect the presence of a predator. In contrast to olfactory cues (from faeces or urine deposited by passing predators), acoustic cues provide greater detection distances and immediate, rather than retrospective, information about predator location. Since eastern quolls forage in long grass and shrubby understorey (M. Jones, pers. obs.), visual cues are probably less important in the early detection of predators, although response to visual cues would be important in escape. We predict that eastern quolls will respond to the species-specific acoustic cues of their sympatric predators, commensurate with the level of danger posed, but will not respond appropriately to cues of the evolutionarily novel fox.

METHODS

Six adult (1.2–1.5 kg) and six juvenile (0.6–0.8 kg) male eastern quolls were collected over summer (between September and March; juveniles collected during the November–December weaning period). Males, rather than females, were used to maximise the juvenile-to-adult size contrast: eastern quolls are sexually size dimorphic and size differences between the sexes increase with age. The site at Kellevie in southeastern Tasmania (42°47'S, 147°46'E) was a mixture of cattle pasture and open eucalypt forest and was chosen for its comparatively dense populations of quolls, Tasmanian devils (*Sarcophilus laniarius*), masked owls (*Tyto novaehollandiae castanops*) and cats (*Felis catus*: Bell, Mooney & Wiersma, 1996; Jones & Rose, 1996): this study was carried out prior to the fox incursions into Tasmania. Tasmanian masked owls prey on both adult and juvenile eastern quolls in open dry forests and adjacent open habitats (Mooney, 1993; Bell *et al.*, 1996). Tasmanian devils are an aggressive and potentially dangerous competitor that may also prey on quolls. We know from wild populations that devils hunt in open forest that quolls frequent (Jones & Barmuta, 2000), that devils eat eastern quolls (Jones & Barmuta, 1998), that the presence of devils enhances vigilance in wild eastern quolls and that devils chase quolls feeding at carcasses (Jones, 1998).

Eastern quolls were trapped overnight on the forest edge in meat-baited, wire cage traps. They were weighed, sexed and individually numbered with an ear tattoo. The animals required were put in to calico bags and transported to an outdoor roofed holding enclosure (four adjacent 2.5 m × 5 m pens, University of Tasmania animal house) where they were kept separately for a 1 week adjustment period prior to the trials. In males of the related Tasmanian devil, plasma cortisol concentrations fall to basal levels after only 48 h in captivity (S. Jones, T. Lockhart and R. Rose, unpub. results) indicating that 1 week is probably a sufficient period for quolls to adjust to captivity. Each individual was transferred to the test enclosure for familiarisation 24 h before observations began. Dry dog food and fresh water were supplied *ad libidum* and each quoll was given one fresh, dead, day-old chick daily. All animals were released at point of capture within 3 weeks of being removed from the wild.

The acoustic experiment was carried out in a 20 m × 15 m, fully-enclosed, wire-mesh, outdoor enclosure, provided with a nest box, water and food, all in the centre. The roof-support poles, placed 3 m apart in a grid, were labelled and used for the estimation of distance moved. An observation hut with a sealed window overlooking the enclosure and a door facing away from the enclosure was located midway along, and just outside, one enclosure fence.

Audio playback techniques (McGregor, 1992) were used to test responses to acoustic cues (vocalisations of active individuals) of four predators: the Tasmanian masked owl (female territorial call; Tasmanian Parks and Wildlife Service tape), Tasmanian devil (feeding interaction vocalisations; ABC Natural History Unit 'Clash of the Carnivores' video), feral cat (contact call to owner; domestic cat), red fox (from moving captive foxes; CSIRO), a sympatric non-predator control (domestic cows, *Bos taurus*, mooing), and a noise stimulus (low monotone noise created by a human voice). The noise stimulus did not result in any behavioural change in the quolls (no significant response between the 'pre-stimulus' and 'noise stimulus' periods; see Results, below). It was, therefore, assumed that the noise stimulus did not represent either a negative or a positive association for the quolls. Predator vocalisations were played back using a tape recorder (AKAI PJ200CD) placed beside the observation shed (within reach of the door so the observer could operate it without leaving the shed) 2 m from the enclosure fence. The quolls did not react to the operation of the tape recorder and player, or to the observer within the shed. Volume was standardised (at level 4) among trials. This approximated natural sound levels (to the human ear) for all acoustic cues.

Behavioural responses were recorded for the 14-min duration of each of six different vocalisation tapes as follows: (1) *Pre-stimulus*–a 5-min period with the tape running but no stimulus, to provide data on baseline behaviour; (2) *Noise stimulus*–2 min of the noise stimulus, to distinguish whether behavioural responses were related specifically to a test stimulus or simply to the presence of a noise; (3) *Test stimulus*–2 min of a test stimulus, designed to simulate the natural duration (short) and pattern (repeated rather than continuous) of predator vocalisations, of one of the following types: either a predator vocalisation (owl, devil, cat or fox), the non-predator control vocalisation (cow), or a continuation of the noise stimulus as a control; (4) *Post-stimulus*–another 5-min period with the tape running but no stimulus. Only the last 2 min of data from the pre- and post-stimulus periods were analysed, to allow for some recovery towards baseline behaviour following the switching on of the tape player (in case this elicited a reaction) and cessation
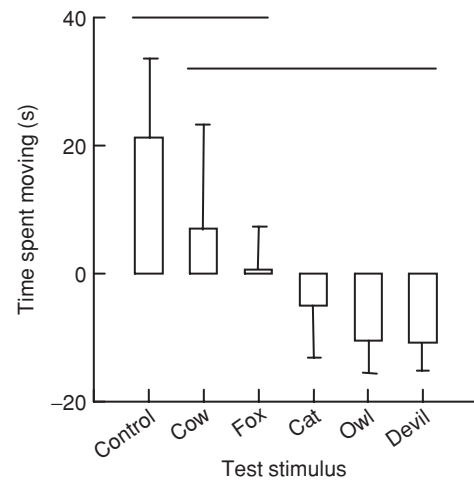
of a predator call, respectively, thereby minimising any confounding of the test responses with the baseline behaviour.

Each quoll was exposed to one of the test stimuli tapes per night over 6 consecutive nights. Each tape was played 45 min after pitch dark, which allowed time for the quolls to complete feeding. Animals were observed using overhead red lights and night vision equipment (DIPOL GB-201). Observations were dictated continuously into a hand-held tape recorder (Sony Microcassette-corder M-729V, Martin & Bateson, 1993), while using a stopwatch to determine the duration of behaviours. The quolls showed no reaction to either the observer or the tape player. Behaviours were recorded as follows: (1) time spent moving (in s)-defined as any locomotory movement (walking or running), excluding time when the quoll was stationary, feeding or grooming; (2) distance moved (in m)-estimated from timed records of the quoll's location in relation to the grid; (3) time spent vigilant (in s)-vigilance was defined as head up, looking around slowly from side to side with ears erect (the beginning and end of a vigilance event was defined as when the position of the head moved above or below the level of the body, respectively) and (4) the number of vigilant events.

Experimental design and statistical analyses

We employed a Latin square design (of $n = 6$; separate squares for adults and juveniles) analysed using a repeated measures cross-over ANOVA (Ratkowsky, Evans & Alldredge, 1993; SAS, 1998). Cross-over designs are a powerful method for statistical compensation when small sample sizes are desirable to reduce impacts on wild populations (D. Ratkowsky, pers. comm.), a major consideration for this and other studies of threatened species. Other designs (e.g. MANOVA) are inappropriate because they lose power at small sample sizes (D. Ratkowsky, pers. comm.). Each row of the Latin square represented a different individual, with each receiving the different test stimuli (predators, control, noise stimulus) on consecutive nights in the order specified by the columns. Individuals and test stimuli were allocated randomly to letters of the Latin square. Use of the Latin square design ensured that each individual (quoll) received the test stimuli in a different order, that each test stimulus was followed by every other one and that any carry-over effect of the previous stimulus could be accounted for statistically. Logistic constraints (one observer and one enclosure) precluded simultaneous testing of all individuals. To ensure similar test conditions, trials were conducted only on fine nights during one summer non-breeding period.

The main effects in the repeated measures cross-over ANOVA were age, individual (within age), night on which the trial was conducted, carry-over from the previous night's treatment and test stimulus. To assess which main effects varied over time (i.e. within subject effects), we used the interaction terms of successive differences between the four stimulus periods (the repeated measures, coded 'interval') by the main effects. An ANOVA of
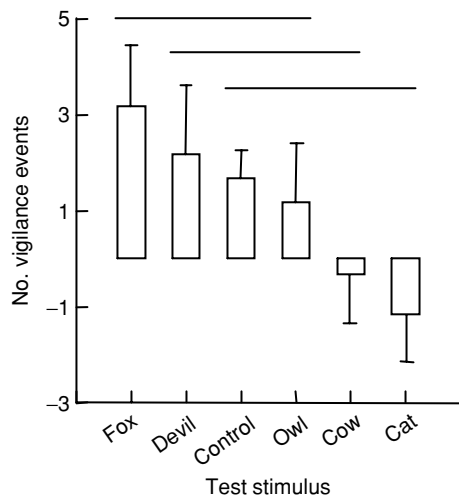

Fig. 1. Differences in the time spent moving by juvenile eastern quolls in the transition from the 'noise' stimulus period to the 'test' stimulus period for each of the test stimuli. Horizontal lines represent significant groupings (Tukey's least squares difference test). Bars represent mean (± standard error).

contrast variables for each of the three intervals indicated in which transitions between stimulus periods (e.g. from noise to test stimulus) any significant differences (nominal $P = 0.05$) lay. To assess significance patterns across different test stimuli (fox, cat, cow, etc), *post-hoc* groupings (Tukey's Least Squares Difference) were generated using a univariate cross-over ANOVA on the difference of the value between the two stimulus periods (e.g. 'predator' stimulus minus 'noise' stimulus). The analyses were run separately on the square-root transformed data for each of the four behaviours.

Initial analyses indicated that age was not a significant effect (e.g. for 'time spent moving': $F = 3.34$, d.f. = 1, $P = 0.0976$), but non-significant bimodality in the data suggested two separate age populations, so all subsequent analyses were conducted separately on adults and juveniles. Carry-over proved to be non-significant in all analyses, so the data were reanalysed with this term deleted from the model.

RESULTS

Juvenile eastern quolls responded strongly to the test stimuli, altering their movement although not their vigilance behaviour. There was very strong evidence for an influence of test stimulus type on the amount of time juveniles spent moving (Interval by test stimulus interaction term: $F = 4.64$, d.f. = 15, $P = 0.0001$). Most of this effect occurred during the transition from the noise to the test stimulus (Interval 2: $F = 3.53$, d.f. = 5, $P = 0.019$), although the behavioural effects of the test stimulus appeared to persist to some degree into the post-stimulus period (Interval 3: $F = 2.77$, d.f. = 5, $P = 0.047$). Tukey's LSD tests indicated a gradation across stimuli of decreasing time spent moving from a maximum value for the noise control, through the non-predator control (cow), the fox, cat, owl and devil, with the response to

Fig. 2. Differences in the frequency of scanning by adult eastern quolls in the transition from the 'noise' stimulus period to the 'test' stimulus period for each of the test stimuli. Horizontal lines represent significant groupings (Tukey's least squares difference test). Bars represent mean (± standard error).

continuation of the noise stimulus being most different from that to the other stimuli (Fig. 1). There was a large variation in response behaviour between individuals (Interval by individual interaction: $F = 3.38$, d.f. $= 15$, $P = 0.0004$), which was strongest in the noise to predator transition (Interval 2: $F = 8.37$, d.f. $= 5$, $P = 0.0002$). There was some effect of night (Interval by night interaction: $F = 1.85$, d.f. $= 15$, $P = 0.048$), but this did not reach significance in any of the three transitions between stimulus periods.

There was a similar, but much weaker, pattern of response to the different test stimuli in the correlated 'distance moved' measure (Interval by test stimulus interaction: $F = 2.21$, d.f. $= 15$, $P = 0.016$; identical ranking of test stimuli in post-hoc tests). Most of the variation in this 'interval by test stimulus' interaction was explained by Interval 2 (noise to test stimulus transition) although this did not reach significance. Juvenile eastern quolls showed no differences in responses to the test stimuli in the amount of time spent being vigilant or in the frequency of scanning. However, individual variation in response was significant (Individual in Interval 2; for 'distance moved': $F = 5.16$, d.f. $= 5$, $P = 0.003$; for 'frequency of scanning': $F = 3.18$, d.f. $= 5$, $P = 0.028$), perhaps obscuring any effect of the test stimulus.

By contrast, adult eastern quolls did not alter their movement behaviour in response to the test stimuli. However, adults showed a weak differential response in their vigilance behaviour to the different types of test stimuli. For frequency of scanning (number of vigilance events), the interval by test stimulus interaction approached significance ($F = 1.73$, d.f. $= 15$, $P = 0.080$), most of the variation of which was accounted for in the transition from the noise to the test stimulus, which all but reached significance at the 0.05 level ($F = 2.87$, d.f. $= 5$, $P = 0.052$). Tukey's post-hoc tests indicate a trend in response of decreasing frequency of scanning from fox, to

devil, to control, to owl, to cow and then to cat, with fox and cat being the most distinctly different (Fig. 2). For the correlated measure of amount of time spent vigilant, there was weak evidence for differences across the stimulus periods (Interval by test stimulus interaction: $F = 1.93$, d.f. $= 15$, $P = 0.038$), although there were no significant changes in any of the individual transitions between stimulus periods. No other effects (individual or night by interval interactions) were significant; neither were there any significant changes in response in transitions between pre- and noise-stimulus (background behaviour to control noise stimulus) or noise- and post-stimulus (test to background behaviour).

DISCUSSION

Eastern quolls display anti-predator responses to sympatric predators (Tasmanian masked owl and Tasmanian devil) commensurate with the perceived predation risk expected for each test stimulus. However, responses vary with age: juveniles show stronger responses than, and exhibit different behaviours from, adults. This is consistent with their smaller body size, their inexperience and their presumed greater vulnerability to predation. They respond to vocalisations of sympatric predators by moving less, which is likely to make them more difficult to detect and be attacked by visual predators (e.g. Kaufman, 1974). In contrast, adult quolls slightly increase their vigilance, which may help them locate the predator before the predator detects its prey. We suggest that the more experienced adults have more flexible responses, whereby freezing and escape responses are instigated only when risk is high, thus reducing the overall energetic costs of anti-predator behaviour via less disrupted foraging. In juveniles, it may be that the vigilance response is suppressed by the strong locomotory response, since the two are somewhat exclusive (the head up vigilant posture may increase conspicuousness, which opposes the benefits of reduced movement).

Eastern quolls do not appear to perceive acoustic cues from the evolutionarily novel foxes as emanating from a dangerous predator. The behavioural responses of juvenile quolls towards sympatric predators was to decrease movement, but they increased movement in response to fox vocalisations as well as to the non-threatening cow vocalisations and control noises. Adult quolls appear to increase vigilance both to detect the location of a predator (devil, owl) and to identify unknown sounds (control noise, fox), which is less informative. The lack of appropriate anti-predator responses to foxes suggests that naïve quolls (at least in juveniles) may not take appropriate evasive action: the predatory impact of foxes is therefore likely to be high. The situation on mainland Australia suggests that both eastern quolls and the similar western quolls (D. geoffroii) are extremely vulnerable to foxes, even 150 years after fox introduction. Western quolls contracted to 3% of their former range (70% of Australia) as fox populations expanded across the continent, which was similar to the extinction pattern

for mainland eastern quolls (Orell & Morris, 1994; Jones *et al.*, 2003). The fact that small populations of western quolls have survived in wetter forests where fox numbers are low (Orell & Morris, 1994), suggests that eastern quolls could persist in wet forest patches if foxes become established in Tasmania. However, the weight of evidence (catastrophic mainland quoll declines in fox presence, recovery and expansion of western quoll populations dependent on fox control: Morris *et al.*, 2003) suggests that ongoing fox control would be an essential component of eastern quoll conservation management in Tasmania and for mainland reintroduction programmes, although anti-predator training of captive-bred animals may be beneficial (see McLean, Lundie-Jenkins & Jarman, 1996; Griffin, Blumstein & Evans, 2000).

Cats appear to represent a lesser threat to eastern quolls than native predators or foxes and their impact is probably greatest on juvenile quolls. The anti-predator behaviours towards cats, the relative responses of juvenile and adult quolls, body size relationships of juvenile and adult quolls and the three mammalian predators and the long coexistence of cats and quolls all support this conclusion. First, juvenile quolls display the same type of response to cats (decrease in movement) as they show towards sympatric predators (devils and owls), whereas adult quolls treat cats like cows (as non-threatening). Second, juvenile quolls are smaller and more likely to be overpowered by cats than are adult quolls. Third, among the mammalian predators, the larger species, devils (6–13 kg) and foxes (4–8 kg), may present a greater risk of predation or fatally aggressive interference competition to quolls than do cats (3–4 kg) (intraguild competitive killings are more common than nutritionally-driven predation among carnivores: Jones, 1998; Van Valkenburgh, 2001; Macdonald, Bryce & Thom, 2001).

The introduction of foxes to Tasmania presents a serious threat of extinction to Tasmania's medium-sized mammalian fauna: as we found for the eastern quoll, all species are likely to lack the appropriate anti-predator responses to the evolutionarily novel fox. In contrast, feral and domestic cats pose a lesser threat, with the predatory impact mainly being on juveniles.

Acknowledgments

REFERENCES

Bell, P., Mooney, N. & Wiersma, J. (1996). *Predicting essential habitat for forest owls in Tasmania*. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee, Tasmanian Public Land Use Commission Report.

Blumstein, D. T., Daniel, J. C., Griffin, A. S. & Evans, C. S. (2000). Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behav. Ecol.* **11:** 528–535.

Brown, J., Laundré, J. W. & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80:** 385–399.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22:** 37–47.

Burbidge, A. A. (1999). Conservation values and management of Australian islands for non-volant mammal conservation. *Aust. Mammal.* **21:** 67–74.

Cardillo, M. & Bromham, L. (2001). Body size and risk of extinction in Australian mammals. *Conserv. Biol.* **15:** 1435–1440.

Caro, T. (Ed.) (1998). *Behavioral ecology and conservation biology*. Oxford: Oxford University Press.

Caughley, G. & Gunn, A. (1996). *Conservation biology in theory and practice*. Cambridge, MA: Blackwell Scientific.

Clemmons, J. R. & Buchholz, R. (Eds) (1997). *Behavioural approaches to conservation in the wild*. Cambridge: Cambridge University Press.

Coss, R. G. (1999). Effects of relaxed natural selection on the evolution of behavior. In *Geographic variation of behavior: an evolutionary perspective*: 180–208. Foster, S. A. & Endler, J. A. (Eds) Oxford: Oxford University Press.

Curio, E. (1996). Conservation needs ethology. *Trends Ecol. Evol.* **11:** 260–263.

Dickman, C. R. (1996*a*). Impact of exotic generalist predators on the native fauna of Australia. *Wildl. Biol.* **2:** 185–195.

Dickman, C. R. (1996*b*). *Overview of the impacts of feral cats on Australian native fauna*. Australian Nature Conservation Agency Report.

Gosling, L. M. & Sutherland, W. J. (Eds) (2000). *Behaviour and conservation*. Cambridge: Cambridge University Press.

Griffin, A. S., Blumstein, D. T. & Evans, C. S. (2000). Training captive-bred or translocated animals to avoid predators. *Conserv. Biol.* **14:** 1317–1326.

IUCN (2003). *2003 Red list of threatened species*. Available at: http://www.redlist.org. Accessed on 8 March 2004.

Johnson, C. N., Delean, S. & Balmford, A. (2002). Phylogeny and the selectivity of extinction in Australian marsupials. *Anim. Conserv.* **5:** 135–142.

Jones, M. E. (1998). Function of vigilance in sympatric marsupial carnivores, the eastern quoll and the Tasmanian devil. *Anim. Behav.* **56:** 1279–1284.

Jones, M. E. & Barmuta, L. A. (1998). Diet overlap and abundance of sympatric dasyurid carnivores: a hypothesis of competition? *J. Anim. Ecol.* **67:** 410–421.

Jones, M. E. & Barmuta, L. A. (2000). Niche differentiation among sympatric Australian dasyurid carnivores. *J. Mammal.* **81:** 434–447.

Jones, M. E. & Rose, R. K. (1996). *Preliminary assessment of distribution and habitat associations of the spotted-tailed quoll (Dasyurus maculatus maculatus) and eastern quoll (D. viverrinus) in Tasmania to determine conservation and reservation status*. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee, Tasmanian Public Land Use Commission Report.

Jones, M. E., Oakwood, M., Belcher, C., Morris, K., Murray, A. J., Woolley, P. A., Firestone, K. B., Johnson, B. & Burnett, S.

(2003). Carnivore concerns: problems, issues and solutions for conserving Australasia's marsupial carnivores. In *Predators with pouches: the biology of carnivorous marsupials*: 418–430. Jones, M. E., Dickman, C. R. & Archer, M. (Eds). Melbourne: CSIRO Publishing.

Kaufman, D. W. (1974). Differential predation on active and inactive prey by owls. *Auk* **91:** 172–172.

Macdonald, D. W., Bryce, J. M. & Thom, M. D. (2001). Introduced mammals: do carnivores and herbivores usurp native species by different mechanisms? In *Advances in vertebrate pest management II*: 11–14. Pelz, H. J., Cowan, D. P. & Feare, C. J. (Eds). Fürth: Filander Verlag.

Martin, P. & Bateson, P. (1993). *Measuring behaviour: an introductory guide*, 2nd edn. Cambridge: Cambridge University Press.

Maxwell, S., Burbidge, A. A. & Morris, K. (1996). *The Action Plan for Australian Marsupials and Monotremes*. IUCN/SSC Australasian Marsupial and Monotreme Specialist Group, Wildlife Australia, Environment Australia, Canberra ACT Australia. Wildlife Australia, Endangered Species Program, Project Number 500 Report.

McGregor, P. K. (Ed.) (1992). *Playback and studies of animal communication*. NATO Advanced Science Institutes Series. New York, London: Plenum Press.

McLean, I. G., Lundie-Jenkins, G. & Jarman, P. J. (1996). Teaching an endangered mammal to recognise predators. *Biol. Conserv.* **75:** 51–62.

Mooney, N. (1993). Diet of the masked owl in Tasmania: past and present. In *Australian raptor studies*: 160–174. Olsen, P. (Ed.). Melbourne: Australian Raptor Association, Royal Australian Ornithologists Union.

Morris, K., Johnson, B., Orell, P., Wayne, A. & Gaikorst, G. (2003). Recovery of the threatened chuditch (*Dasyurus geoffroii* Gould, 1841): a case study. In *Predators with pouches: the biology of carnivorous marsupials*. Jones, M. E., Dickman, C. R. & Archer, M. (Eds). Melbourne: CSIRO Publishing.

Morton, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proc. Ecol. Soc. Aust*. **16:** 210–213.

Orell, P. & Morris, K. (1994). *Chuditch recovery plan, 1992–2001*. Western Australian Department of Conservation and Land Management, Western Australian Wildlife Research Centre. Wildlife Management Program Report No. 13.

Ratkowsky, D. A., Evans, M. C. & Alldredge, J. R. (1993). *Cross-over experiments*. New York: Marcel Dekker Inc.

Rolls, E. C. (1969). *They all ran wild*. Sydney: Angus and Robertson.

SAS (1998). SAS (r) Proprietary Software Release 6.12 TS020. Cary, NC: SAS Institute Inc.

Short, J., Bradshaw, S. D., Giles, J., Prince, R. I. T. & Wilson, G. R. (1992). Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia–A review. *Biol. Conserv*. **62:** 189–204.

Short, J. & Smith, A. (1994). Mammal decline and recovery in Australia. *J. Mammal*. **75:** 288–297.

Van Valkenburgh, B. (2001). The dog-eat-dog world of carnivores: a review of past and present carnivore community dynamics. In *Meat-eating and human Evolution*: 101–121. Stanford, C. B. & Burn, H. T. (Eds). Oxford: Oxford University Press.