Nocturnal behaviour of the parma wallaby, *Macropus parma* (Marsupialia : Macropodoidea)

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Abstract

Commercial night-vision devices permit the study of nocturnal behaviour without visible light sources, obviating concerns about the effects of supplemental lighting on natural behaviour. We used an inexpensive image intensifier to document the previously unstudied nocturnal behaviour of the parma wallaby, *Macropus parma* Waterhouse, 1846, based on a captive population of 6 male and 6 female sexually mature wallabies. A total of 150 h of observation was conducted over 34 nights and 6 days. The circadian rhythm of this species was grossly similar to that of many other Macropodoidea, although there was a pronounced peak in activity at dawn. The behavioural time budgets of males and females were reliably different, with males spending more time actively foraging than females. Social interactions were rare in both sexes, but we were able to characterise sexual behaviour in detail. Courtship typically began with sexual checking of the female by the male, after which the male pawed the female's rump repeatedly. This was occasionally followed by mounting and copulation, but typically the male presented his chest, drawing the female's head toward it with his forepaws. While this 'head rubbing' is clearly homologous with components of social behaviour in other wallabies, it seems uniquely elaborate in parmas. Interactions between males and females were accompanied by characteristic vocalisations. Males produced repeated broad-band 'clucking' sounds while grooming females, who often responded by hissing. The structure and context of these signals suggest that clucks function to stimulate the female, while hisses probably encode threat. It is likely that males produce both olfactory and acoustic signals during courtship; such cues could play a role in mate choice decisions by females. Our results demonstrate that nocturnal observations on small macropodids are feasible and suggest that more reliable information about social behaviour is obtained at night.

Introduction

In Australia, the most familiar of the marsupials are the Macropodoidea, which include the kangaroos, wallabies and rat-kangaroos (Warburton and Sadleir 1990). Within this super-family, animals range in size from small hare-wallabies weighing 1 kg to the red (*Macropus rufus*) and the eastern grey (*M. giganteus*) kangaroos weighing more than 80 kg (Hume *et al.* 1989). The ranges of these species cover much of the Australian continent from the arid zone to coastal brush and tropical forests (Hume *et al.* 1989). Given this range in morphology and habitat use, it is not surprising that there is also considerable heterogeneity in social behaviour (see Jarman 1991 for a review). There is a degree of patchiness in research, in part because some species are more readily accessible and present fewer logistical problems than others (Coulson 1989). While some of the larger macropods have been studied extensively, much less is known about the behaviour of many of the smaller species, some of which present particular problems for observational work. Generalisations about social and aggressive behaviour are based instead upon patterns apparent in species such as the red and eastern grey kangaroos (e.g. Grant 1973; Croft 1985; Croft and Snaith 1991). Observational data on a wider range of macropods are thus of theoretical value because they will provide the basis for systematic comparative studies.

The parma wallaby, *Macropus parma* Waterhouse, 1846, is the smallest member of the genus *Macropus* (King 1990). The species was considered extinct until it was rediscovered in the Gosford district in 1965 (Maynes 1974) along with a feral population on Kawau island off New Zealand in 1967 (Maynes 1977*a*). The parma wallaby was placed under protection by the

International Union for the Conservation of Nature between 1969 and 1984 (King 1990). Today, numbers have increased, but although parma wallabies can be locally common, the species is still considered to be rare (Read and Fox 1991). Zoo populations have to be managed carefully and the success of these programs may be substantially enhanced by improved understanding of social behaviour, particularly agonistic interactions and courtship (Herter *et al*. 1985).

We are aware of only one previous study examining the behaviour of the parma wallaby. Herter *et al.* (1985) described the behavioural repertoire of a small social group maintained in Munich Zoo on the basis of observations conducted during the day. There has been no systematic analysis of the circadian pattern of activity in this species, although Maynes (1977*b*), when conducting a census, noted that fewer animals were visible during the day. It has been assumed that parma wallabies are nocturnal because this is the typical pattern in other macropods (Croft 1989).

Despite the likely importance of nocturnal social interactions, there are only a few reports that include observational data collected at night (Stodart 1966; Russell 1970*a*, 1970*b*; Grant 1973; Coulson 1978; Johnson 1980; Proctor-Gray and Ganslosser 1986). Most of this work was conducted using visible spotlights or floodlights, which raises concerns about whether the behaviour of the study animals might have been affected. A less intrusive alternative approach involves the use of image intensifiers, but these have, until recently, been both expensive and difficult to obtain. Only a handful of researchers have had access to night-vision devices (Croft 1985; Clarke *et al*. 1989; Croft and Snaith 1991; Watson and Dawson 1993; Clarke *et al*. 1995), and even in these studies it was necessary to use visible-light sources to illuminate the field of view.

Our aim in the present study was to describe quantitatively the nocturnal behaviour of the parma wallaby. We wished particularly to take advantage of the recent availability of inexpensive commercial night-vision devices to conduct observations with minimal intrusion. A secondary goal was to assess the technical feasibility of such an approach with small macropods.

Materials and Methods

Housing and study animals

We used two pens in the Macquarie University Fauna Park for behavioural observations. Each pen had an area of approximately 280 m^2, and contained a single feed bin (normally open every other day) and a drinking trough. Cover (consisting of wood piles, brush and wooden lean-tos) was supplied in both pens and arranged to allow a maximum field of view from the hides used for observations. We positioned the hides so that the observer could enter and leave them without moving through the pen, thereby minimising disturbance to the study animals. Three male and three female sexually mature captive-bred parma wallabies were housed in each pen, providing a total study population of 12 animals. We designed social groups to simulate natural variation in body size (Table 1).

Observational aids

We used an NV100 'nightviewer' image intensifier (Apple Nighteyes) mounted on a tripod for all nocturnal observations. This device provides an optical magnification of 3.8 and amplifies incident light by a factor of 10 000. The nightviewer is also fitted with an infra-red 'laser' spotlight, invisible to the naked

Table 1. Composition of social groups
Initial weights (kg) of individual animals listed in order of dominance status

| | Group A | | Group B | |
	Male	Female	Male	Female
α	6.0	3.2	5.0	3.1
β	4.2	3.3	3.8	2.9
γ	3.2	3.7	3.5	3.1

eye, which can be used for supplemental lighting. Daytime observations were conducted with 9×30 binoculars. To time observation periods, we constructed a simple electronic device (Dick Smith: Multi-timer module) that provided a brief flash of red light in the periphery of the observer's visual field at specified intervals. All observations were recorded on a dictaphone mounted above the image intensifier.

Individually distinctive collars were made for each wallaby from small dog collars and reflective tape. Initially, animals became abnormally active and made obvious attempts to remove the collars. However, the wallabies habituated quickly and, after a period of not more than 2 h, the collars did not appear to affect their behaviour. Previous studies have used visible spotlights to illuminate reflective markers. We found that this was unnecessary because the infra-red 'laser' illuminator was sufficient to permit recognition of collar patterns.

Observation times

To determine the best time for data collection, we began by doing all-night and all-day observations for each pen. Group scans (Altmann 1974) at 5-min intervals were conducted over six 2-h observational blocks: at sunset, over midnight, before and after dawn, at midday and at dusk. A total of six all-night observations and six all-day observations was completed.

Analysis of this initial data set revealed that the best time for observing social interactions was just prior to dawn. All subsequent observations were conducted between approximately 0230 and 0630 hours. Starting times were adjusted to compensate for changing day length, so that observations consistently ended within 15–20 min of dawn, after which it was too light to use the image intensifier.

Data collection

Behaviour was observed during 10-min focal samples (Altmann 1974). Each animal in a social group was observed twice during the course of an observational block, producing a total of 12 focal sampling periods each night. The sequence in which animals would be selected for observation was determined randomly at the beginning of each block. We conducted a total of 11 nights of 3-h observational blocks resulting in approximately 2 h of direct observations for each pen. Additional time was required for locating focal animals and checking equipment between focal sampling periods. All focal sampling observations were entered into 'The Observer' event-recorder program (Noldus Inc.) in real time from dictaphone audio tapes. This software was then used for sequential analyses and calculation of time budgets (Lehner 1979).

Dominance was measured during 2-h observational blocks over three nights for each pen. Feed bins were kept closed for two days and opened at the start of each observational period. All aggressive interactions between individuals at feed bins and the 'winners' and 'losers' in each were recorded. 'Losers' were categorised by being recipients of physical threats (hitting, biting and snapping) with little or no retaliation, or by displacements (avoiding an approaching conspecific or ending an aggressive interaction by retreating). We tested for the presence of a dominance hierarchy using Landau's index of linearity (Martin and Bateson 1993).

We conducted observations on each social group on alternate nights. Data collection began 15 min after entering the hide to allow the animals to become habituated to the observer's presence. From 19 August to 20 October 1997 we accumulated a total of 150 h of observations over 34 nights and 6 days.

During the course of the study, we noted that both males and females vocalised during courtship interactions. To characterise fully all aspects of courtship behaviour, including acoustic signals, we made opportunistic recordings of these sounds using a Sennheiser MKH 816 directional microphone and a Marantz PMD 222 portable cassette recorder.

Sound analysis

Analogue signals were digitised with an Audiomedia III A/D board (44.1 kHz sampling frequency, 16-bit amplitude encoding) and filtered (high-pass 500 Hz) to attenuate low frequency environmental noise; exploratory analyses demonstrated that there were no signal components in the range covered by the filter stopband. Sound structure was then examined in detail using Canary v 1.2.1 (Cornell Bioacoustics Program).

Statistical analysis

All comparisons were conducted with non-parametric tests, as the number of animals available for study was small and the data were not normally distributed. On pooled data, Friedman ANOVAs were used for three or more samples and Mann–Whitney U-tests for two-sample comparisons. We used an α level of 0.05 throughout.

Results

Circadian rhythm

We observed pronounced variation in activity over the course of each 24-h period (Fig. 1). The proportion of time spent feeding was consistently high throughout the night, but declined sharply at dawn and reached a minimum at midday (Fig. 1*a*). From dawn onwards, the wallabies began to spend long periods sheltering in cover. This inactive behaviour was most pronounced at midday and continued until late afternoon, when the animals began to move out into the open again to graze (Fig. 1*b*). For purposes of this analysis, we considered together all types of non-feeding activity, including social interactions, alert postures and movement. The frequency of these behaviours was relatively low through most of the night but peaked noticeably just before dawn, when grazing was replaced by increased movement about the pens (Fig. 1*c*). There was an increase in social behaviour associated with these changes in levels of alertness and locomotion, and the majority of interactions were observed during this period. Friedman non-parametric
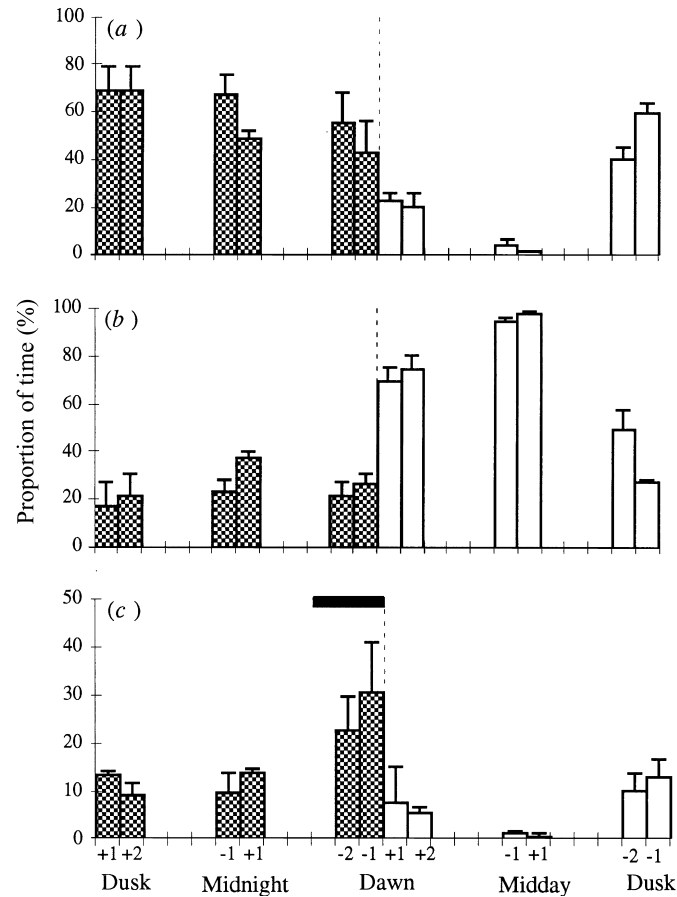
Fig. 1. Circadian rhythm in the parma wallaby. (*a*) Feeding behaviour (graze, drink and feeding from food bin), (*b*) inactive behaviour (crouching, hiding, sleep/doze) and (*c*) active behaviour (alert postures, movement and social behaviour). Note that the vertical axis of panel (*c*) has a different scale from panels (*a*) and (*b*). Horizontal axis of all panels denotes hours (plus or minus) over each period of the day. Error bars represent ± 1 s.e. Horizontal marker in panel (*c*) indicates the period during which data on social behaviour were collected.

ANOVAs reveal that feeding, inactive and active behaviour all varied significantly across a 24-h period (feeding: $\chi^2 = 102.005$, d.f. = 11, $P < 0.0001$; inactive: $\chi^2 = 79.323$, d.f. = 11, $P < 0.0001$; active: $\chi^2 = 74.49$, d.f. = 11, $P < 0.0001$).

Dominance

The two social groups had Landau's indices of linearity (h) of 0.68 and 0.87, respectively. An h value of 1.0 represents a perfect linear hierarchy, while a value of 0.9 or greater is conventionally considered to indicate the presence of a strong linear hierarchy (Martin and Bateson 1993). In both pens, the largest male was the most dominant and would only tolerate the presence of females while feeding. When the sexes were compared separately, males in both pens had a strong linear hierarchy ($h = 0.96$, $h = 1.0$), as did the females ($h = 0.84$, $h = 1.0$).

Behavioural time budgets

Analyses of the amount of time spent engaging in different types of behaviour were conducted using pooled data from both social groups. We concentrated on data obtained from the observations just before dawn, as this was the period of peak social interaction (Fig. 1c). Behaviour was assigned to six categories (feeding, resting, hide, alert, locomotion and social) to provide more detail than was available from the scheme used for analyses of circadian rhythm. Both males and females spent more time in feeding than in any other state. Social behaviour was rare, accounting for only 2.3% of total time in males and 1.6% in females (Fig. 2). There was significant variation in the allocation of time across behavioural categories in both males and females (males: $\chi^2 = 28.10$, d.f. = 5, $P < 0.0001$; females: $\chi^2 = 19.81$, d.f. = 5, $P = 0.0014$). There is also evidence of a sex difference in time budgets. Males tended to spend substantially more time feeding than in resting, hide, alert and locomotor behaviours. In contrast, females
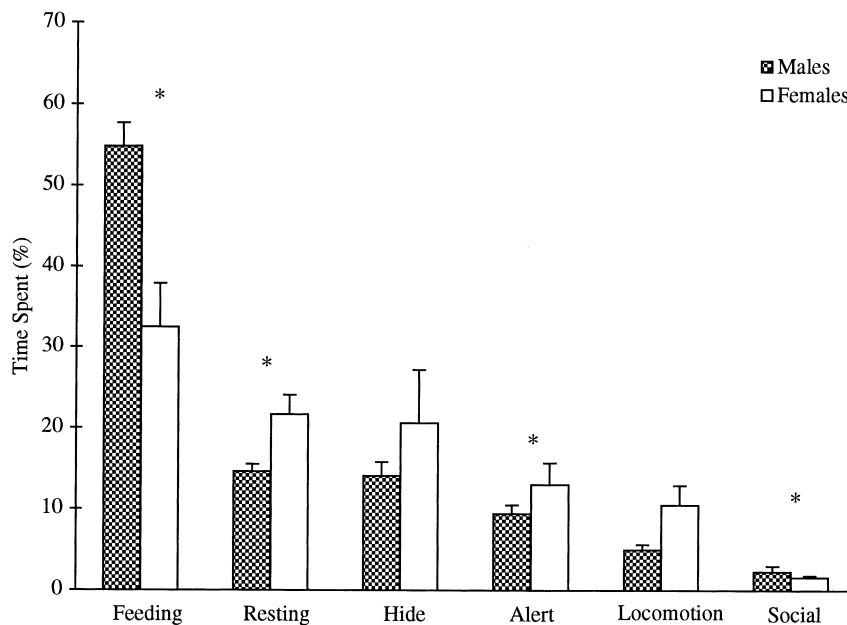
Fig. 2. Behavioural time budget of the parma wallaby. The feeding category is the same as that in Fig. 1. Resting behaviour includes all components of inactive behaviour, except hiding in cover which is represented separately. Alert includes vigilance behaviour such as scanning, sniffing the air and alarm thumping. Locomotion includes walking and hopping, while social behaviour includes all interactions between individuals. Error bars represent + 1 s.e. Asterisks denote significant differences ($P < 0.05$).
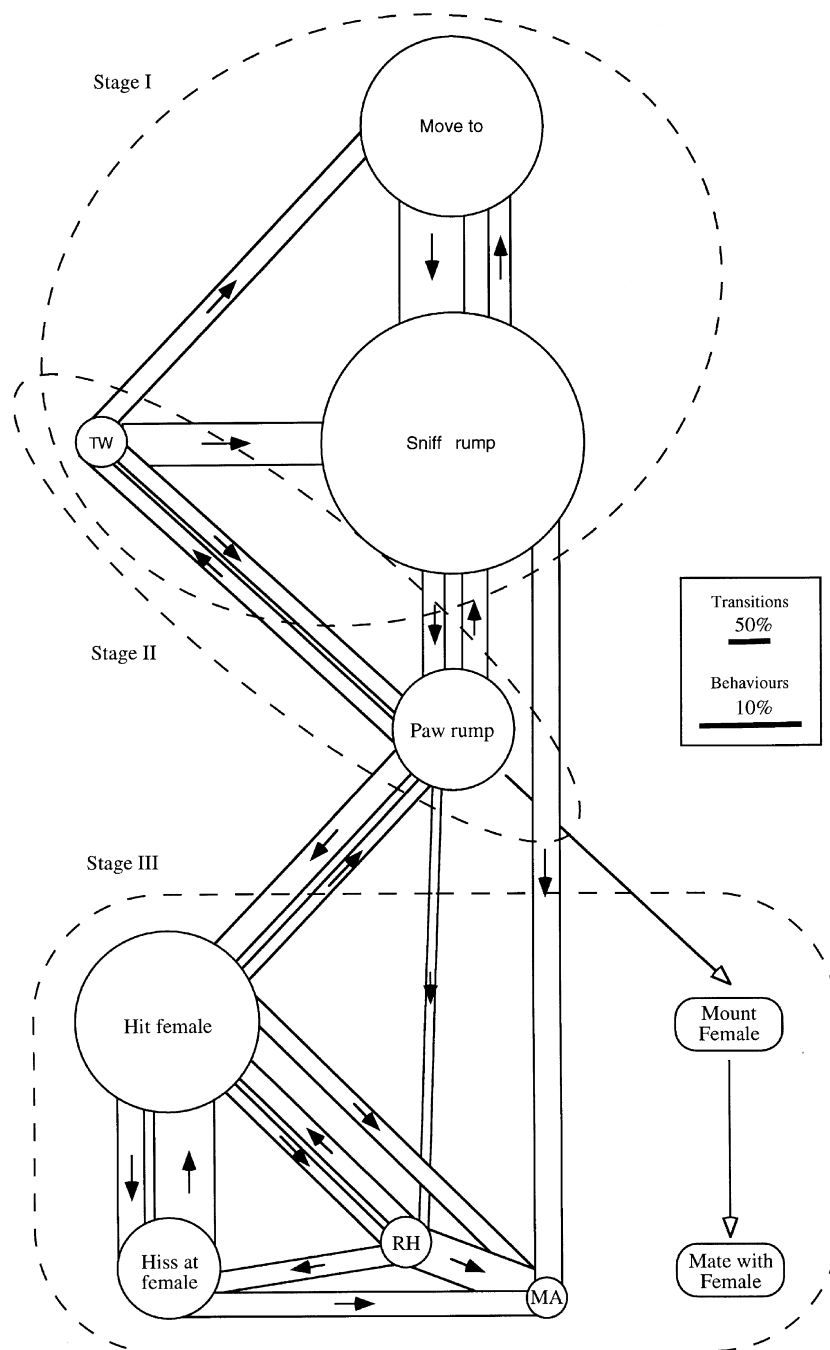
Fig. 3. An ethogram summarising the relationships between components of parma wallaby courtship behaviour determined from sequential analysis. Each of the three main stages are also indicated. The key represents the frequency scale at which behavioural transitions and behaviours occurred. Though no transitions below 10% are included, 'mount female' and 'mate with female' are shown to indicate their location in the courtship sequence. TW = tail wag, RH = head rub and MA = move away from female.

distributed their time more evenly between behavioural categories, spending a larger proportion of their time than males in four of the five non-feeding states. The differences between males and females in time allocated to feeding (Mann–Whitney U-test: $U = 55.0$, $n = 6$, $P = 0.013$), resting ($U = 25.0$, $n = 6$, $P = 0.0306$) and locomotion ($U = 22.0$, $n = 6$, $P = 0.0082$) were all statistically significant.

Courtship behaviour

We conducted sequential analyses of all observed social interactions, focussing particularly on sexual behaviour. Quantitative descriptions allowed us to identify the characteristic components of courtship sequences and the predictive relationships between them. Courtship in parma wallabies proceeded in three distinct stages (Fig. 3).

The male initially approached the female and sniffed her cloaca or the region around the base of her tail ('sniff rump'; Fig. 3). Sexual checking was often accompanied by rapid movements of the male's tail ('tail wag') and sometimes by flicking of the forepaws ('paw quiver'). Although it does not appear in Fig. 3 because of its low frequency, 'paw quiver' occurred only during courtship. Both 'tail wag' and 'paw quiver' are likely correlates of heightened sexual arousal in the male, as an erect penis was typically observed from this point onward in the courtship sequence. In many cases, the female responded aggressively, hissing or hitting at the male with her forepaws. Males often responded by striking females in the same way, and such an exchange of blows sometimes ended the courtship sequence.

In the second stage of a courtship sequence, the male began rapidly to paw the rump of the female ('paw rump'; Fig. 3), sometimes with sufficient force to remove tufts of hair from her back and hindquarters. Rump pawing was typically accompanied by soft clucking sounds produced by the male (Fig. 5). This vocalisation seems to be specific to courtship; it was not recorded in any other context. Bouts of tail wagging often preceded and followed rump pawing.

In the final stage of courtship, receptive females leaned forward on their forepaws and allowed the male to mount. Mating was observed only three times. In each case, it immediately followed a bout of rump pawing and was terminated by the female moving away. More commonly, the male moved around to face the female and performed a 'head rub' (Fig. 4). Here

Fig. 4.   A male parma wallaby performing a 'head rub' with a female.
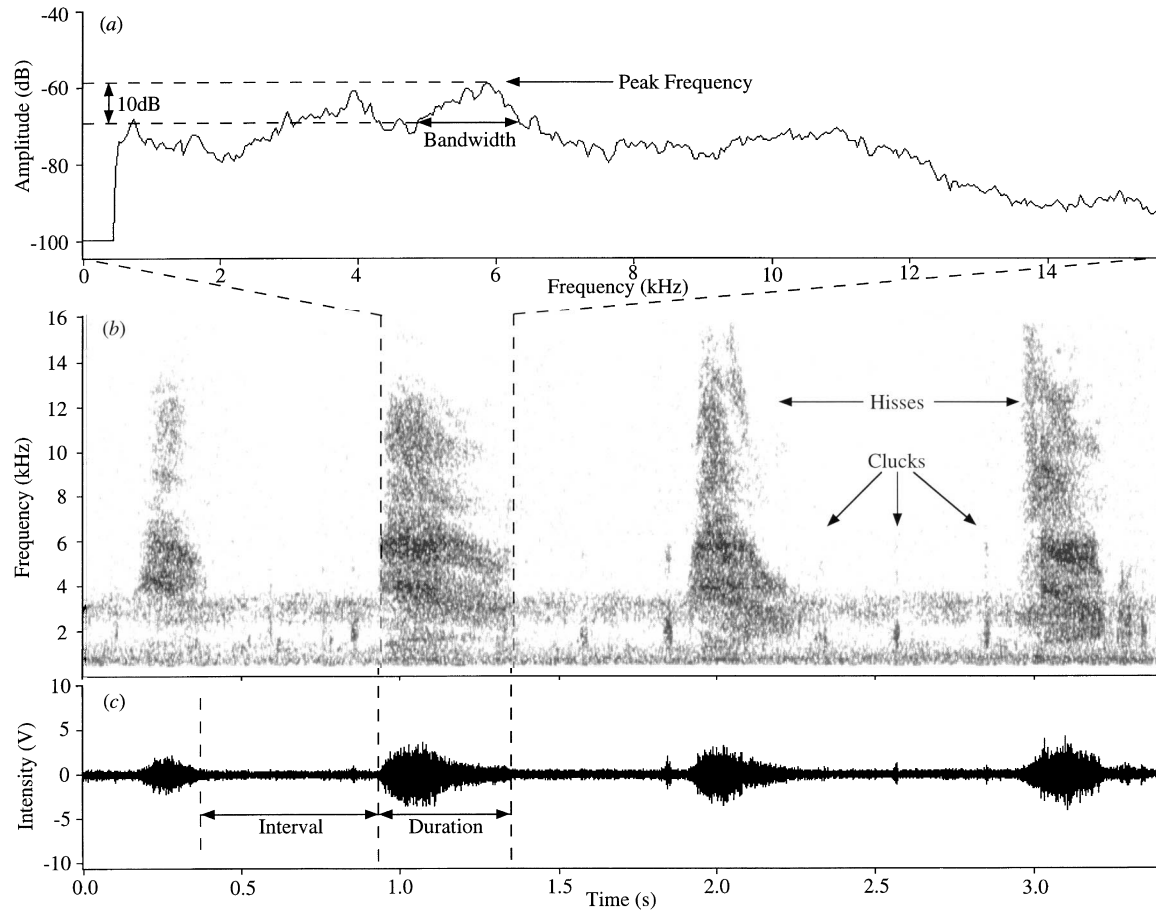
Fig. 5. Clucking and hissing sounds recorded during courtship interactions. (*a*) Mean spectrum of a female hiss generated with 1024 point FFTs (resolution 174 Hz). Peak frequency and bandwidth measurements are indicated. (*b*) Spectrogram generated from overlapping 512 point FFTs (Hanning window; frequency resolution 350 Hz). Spectrogram greyscale represents 40 dB. Continuous sounds at approximately 1 kHz and 3 kHz are environmental noise. (*c*) Oscillogram showing measurement of pulse interval and duration.

the male appeared to position the head of the female using repeated lateral slapping movements with his forepaws, while presenting his chest. The female sometimes responded by lifting her head and sniffing the male's chest. More commonly, head rubbing evoked hissing and snapping from the female.

Vocalisations

The male and female vocalisations recorded during courtship interactions were qualitatively distinct (Fig. 5). Female hisses were long duration sounds with a very large frequency bandwidth and a slow repetition rate. Male clucks were brief pulsatile sounds, which were comparatively narrow band and produced at a substantially higher rate (Table 2).

Table 2. Structure of female hisses and male clucking

Values are mean ± 1 s.e. with the number of vocalisations measured in brackets. Bandwidth is 10 dB down from peak frequency

	Peak frequency (Hz)	Bandwidth (Hz)	Duration (ms)	Interval (ms)
Hiss by female	2520.0 ± 197.0 (77)	1216.8 ± 80.2 (77)	302.2 ± 15.2 (79)	1650.0 ± 335.0 (62)
Cluck by male	2248.0 ± 210.0 (38)	370.7 ± 34.3 (38)	34.8 ± 1.3 (38)	542.2 ± 88.2 (35)

Discussion

We have been able to analyse the circadian rhythm of the parma wallaby and have described several aspects of social and sexual behaviour for the first time. Our results suggest that there are characteristic sex differences in behavioural time budgets and hint at the presence of acoustic and olfactory signals that mediate courtship interactions. In addition, we have been able to assess the technical feasibility of observational work with inexpensive night-vision equipment.

Our principal goal in this study was to examine the nocturnal behaviour of the parma wallaby. With the possible exception of the small rat-kangaroo *Hypsiprymnodon moschatus,* all macropodoids are active during the night (Croft 1989) and spend most of the day resting (Clarke *et al*. 1989; Dressen 1993). The distribution of foraging behaviour in our groups of parma wallabies was consistent with this pattern (Fig. 1*a*), although the observed pre-dawn peak in activity (Fig. 1*c*) is relatively unusual. Many species have a crepuscular pattern, but only a few have been reported to be particularly active at dawn. A captive rock wallaby, *Peradorcas concinna,* kept on an artificial light cycle, was found to become increasingly active at dawn (Goldstone and Nelson 1986) and similar results have been reported for the Bennett wallaby, *Macropus rufogriseus rufogriseus* (equivalent to *Wallabia rufogrisea frutica*), in which changes in activity levels coincided with the period during which most social behaviour occurred (LaFollette 1971). The occurrence of a peak in alert postures and movement at dawn deserves further examination, which might ideally include observations of an undisturbed natural population. We cannot exclude the possibility that the changes in activity levels observed in our enclosures were in part an artefact of captivity, for example as a response to increased environmental noise caused by traffic, although this would not explain the absence of such an effect in the early evening when conditions were similar.

Our finding that the largest male was the dominant individual in both social groups (Table 1) suggests that parma wallabies fit the general pattern in Macropodoidea of a reliable correlation between dominance status and body weight (Packer 1969; Russell 1970*b*; Grant 1973; Morton and Burton 1973; Taylor 1983; Croft 1985; Jaremovic and Croft 1991). Similarly, when the social relationships among males and females were analysed separately, there were strong linear hierarchies apparent for both sexes, as is common in other macropods (Grant 1973; Kaufmann 1975; Croft 1981; Rudd 1994).

During the pre-dawn period in which activity was maximal, both males and females allocated more time to feeding than to any other category of behaviour (Fig. 2). Social interactions were rare. Despite these overall similarities in time budgets, there were clear sex differences. Males spent almost twice as much time as females in feeding, while females spent more time in resting, hiding, moving about, and adopting 'alert' postures (Fig. 2). There are several possible explanations for this pattern, which are not mutually exclusive. Males may simply need to spend more time feeding because they have greater energetic requirements, perhaps as a correlate of their larger body size. Sexual dimorphism is, however, less pronounced in parma wallabies than in many other macropods, so such an explanation, while consistent with the data, does not seem sufficient to account for the magnitude of the observed difference. It is also possible that females are more vulnerable to predation than males and spend more time hiding and in vigilance behaviour for this reason, but we know of no data on sex differences in predation rates with which such a model could currently be tested. Finally, the sex difference in behavioural time budgets may be attributable to social factors, particularly sexual behaviour. The most common response to courtship attempts by males was for the female to move away. It seems likely that unreceptive females spent more time in cover at least in part because of efforts to avoid males, in which case courtship attempts might impose significant costs in terms of reduced foraging opportunity.

We were able to characterise sexual behaviour in some detail, and it is interesting to compare the sequences observed with descriptions of courtship interactions in other macropods. Males initiated courtship by approaching females and sniffing the cloacal region. Such sexual checking is widespread in macropods and probably provides information about the female's oestrous state, which is the principal determinant of responsiveness (Jarman 1991; Ganslosser 1995). We did not see males inspecting the female's pouch, as occurs in other macropods (Poole and Pilton 1964), and parma wallaby females did not respond to sexual checking by urinating, as has been documented in the agile wallaby, *M. agilis* (Dressen 1993).

Tail wagging by males was common during the initial approach to a female and continued through later stages of courtship. This behaviour seems to be restricted to the smaller species. It has also been seen during courtship in the rufous rat-kangaroo, *Aepyprymnus rufescens* (Johnson 1980), the agile wallaby (Dressen 1993) and the whiptail wallaby, *M. parryi* (Kaufmann 1974), and is often coupled with a penile erection. We also observed parma wallabies tail wagging while in alert postures when they were not associating with females, which suggests that such movements reveal high levels of general arousal and are not specific to the courtship context.

Head rubbing is perhaps the most striking feature of the courtship sequence in parma wallabies (Fig. 4) and does not appear to be represented in the same form in other species. There are, however, clearly homologous behaviours. For example, male whiptail wallabies will often face a female and paw, hit or sniff towards her, while bobbing their heads back and forth, sometimes with the nose pointing up and throat bared (Kaufmann 1974). Similar behaviour has been described in both the antilopine wallaroo, *M. antilopinus* (Croft 1982), and the red kangaroo (Wilhelm and Ganslosser 1989), though the male simply displays his ventral surface and erect penis to the female. In another species, the quokka, *Setonix brachyurus,* the most pronounced behaviour between the sexes consists of a female appearing to sniff at the chest of a male, while he stands erect with forelimbs extended (Packer 1969). Morton and Burton (1973) witnessed male Tasmanian pademelons, *Thylogale billardierii*, standing at full height with the head raised in front of the female. The female would then raise her head until it was under the male's or until the male cuffed her into doing so. Such behaviour was often followed by the male attempting to mount. In grey kangaroos, *M. giganteus* (equivalent to *M. canguru*), males frequently paw the head of the female during courtship (Poole and Pilton 1964), and in the closest relative of the parma wallaby, the black-striped wallaby, *M. dorsalis*, males hug females from the front, while pushing their chests up against them (Heathcote 1989).

In some macropods, chest rubbing is directed toward inanimate objects, rather than conspecifics, and this suggests a possible scenario for the evolution of head rubbing in parma wallabies. Croft (1981) reported that male euros, *M. robustus erubescens,* would often grasp a

low shrub or tussock and rub their chest against it while in the company of an oestrous female. Male grey dorcopsis wallabies, *Dorcopsis luctuosa*, have been observed performing a similar display, which involved standing erect against a tree and rubbing the chest briefly up and down it (Bourke 1989). Most macropods have sternal scent glands, implying that many of the behaviours described above deposit an olfactory signal. We speculate that the origin of head rubbing in parma wallabies may have been in scent-marking of inanimate objects, as in more primitive macropods (e.g. Bourke 1989).

Most previous studies have concentrated on the structure of distress vocalisations produced by pouch young separated from their mothers, and on the larger species, such as the red and eastern grey kangaroos (Russell 1973; Baker and Croft 1993). We believe that the present study is the first to quantify the structural characteristics of macropod hissing and clucking vocalisations produced during courtship interactions. The structure of hisses is consistent with the prediction made by Morton's 'motivational–structural rules' model that vocalisations produced by hostile animals should be harsh broad band sounds (Morton 1977). We think it likely that hissing is used as a graded threat signal by females, with the level of threat proportional to rate and intensity. Testing this hypothesis will require a larger set of recordings and behavioural observations, so that it is possible to conduct quantitative analysis of the relationship between structural variation in hisses and the probability of aggressive behaviour. Clucking in male parma wallabies consists of brief rapidly repeated pulses that have an intriguing similarity to the sounds used by humans to stimulate a wide range of domesticated animals (McConnell 1991). These structural properties, together with the context in which the sounds are produced, suggest that clucking functions to increase female receptivity.

Recently, Radford *et al*. (1998) found that captive female red-necked pademelons, *Thylogale thetis*, associate preferentially with larger males when in oestrous, suggesting the occurrence of active mate choice by females. Similarly, some female rock wallabies seek extra-pair copulation with males that have slightly greater forearm length than their mate (Spencer *et al*. 1998). Size differences between males and females are not as pronounced in parma wallabies as in many other macropods (Jarman 1989), and it would be of some comparative interest to assess the relative importance of intrasexual competition between males and female mate preferences in this species. Our observations of head rubbing (Fig. 4) and clucking (Fig. 5) by males imply the use of olfactory and auditory signals during courtship. There is clearly the potential for such cues to interact with an assessment of gross morphology to influence female mate choice decisions.

A secondary goal of the present study was to test the feasibility of collecting observational data on the behaviour of small nocturnal macropods using a commercial night-vision device. Previous studies have been largely confined to observations conducted during the day. Our results suggest that it will be difficult to draw general inferences about behaviour from such data sets because rare social interactions are likely to be under-represented. In our groups of captive parma wallabies, several types of social behaviour were seen only at night. We found that the image intensifier used, although inexpensive, was entirely adequate for our purposes. Observations could be conducted without supplemental visible lights, which allowed us to minimise the degree to which the process of data collection disturbed the behaviour of subject animals.

We suggest that future observational studies on macropodoids should ideally include nocturnal observations to obtain a complete and unbiased record of behaviour. Such information has the potential to improve the conservational status of rare and threatened species by facilitating the development of management strategies that take into account natural patterns of activity and social behaviour.

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