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Identifying the reproductive state of female Julia Creek dunnarts (*Sminthopsis douglasi*) by behavioural observations

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Abstract

The Julia Creek dunnart (*Sminthopsis douglasi*) is an endangered carnivorous marsupial. A recovery plan for the species has been initiated by Queensland Parks and Wildlife Service, which includes captive breeding. An important factor in breeding *S. douglasi* is the identification of oestrus. The current method to identify oestrus consists of examining urine samples for presence of cornified cells. To collect urine, the animals have to be removed from their cages and restrained. This method is stressful for the animals, as well as time consuming. The aim of this study was to identify specific behaviour of *S. douglasi* associated with oestrus, which could be readily observed without the need for handling the animal. This would provide a non-invasive way of identifying oestrus, which would facilitate breeding the species in captivity and planning conservation programs.

Behaviour of *S. douglasi* was observed throughout the night by video recording. The most striking result was the increase in activity of the female when she was in oestrus compared to non-oestrus. The most informative behaviour to observe was entry by the female into the nest box and the frequency with which she entered the area closest to the wall of the enclosure. A discriminant function analysis generated an equation with an over-all predictive power (OPP, the probability of making an accurate identification of reproductive state) of 89%. This result was obtained by watching two random five-minute periods of activity. The equation was tested and verified with new individuals and attained a similar level of OPP. However, the equation was less accurate when the observed female's social context was changed from being housed adjacent to a male, to being accompanied by another female or housed singularly. Consistent with the sensitivity of activity levels as an indicator, the distance run in an exercise wheel was also a good predictor of oestrous state. Females ran a significantly longer distance in their exercise wheel when in oestrus compared to non-oestrus ($p<0.001$).

CERTIFICATION OF DISSERTATION

I certify that the ideas, experimental work, results, analyses, software and conclusions reported in this dissertation are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original and has not been previously submitted for any other award, except where otherwise acknowledged.

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Signature of Supervisor/s	Date

Contents

List of Tables

List of Figures

List of Appendices

List of Abbreviations

Abbreviation	**Meaning**
DFWP	David Fleay Wildlife Park, Burleigh Heads, Queensland
IUCN	International Union for Conservation of Nature
AS	Activity score
NPP	Negative predictive power
OPP	Over-all predictive power
PPP	Positive predictive power
QPWS	Queensland Parks and Wildlife Service
R^2_c	Canonical correlation square
USQ	University of Southern Queensland

Chapter 1

Review of the literature on *S. Douglasi* and other species of the Dasyurid family

1.1 This study

The Julia Creek dunnart (*Sminthopsis douglasi*) is an insectivorous dasyurid marsupial occurring in a restricted range of habitat in the Mitchell grass plains in the semi-arid inland of Australia. It is classified as endangered (IUCN 1996) and has been bred in captivity for conservation purposes since 1992 (Lundie-Jenkins & Payne 2001). Breeding *S. Douglasi* in captivity requires a reliable method to identify oestrus in females. Currently this is done by restraining the animals and collecting urine for examination for the presence of cornified cells. This can be stressful for the animals as well as time consuming. In this study, specific behaviours of *S. douglasi* that are correlated with oestrus and a method is outlined to identify oestrus with a high reliability in a reasonably short period of observation. The ability to detect oestrus by merely observing behaviour is a non-invasive way to enhance the success of breeding the species in captivity and improve our understanding of the reproductive biology and behaviour of *S. douglasi*.

1.2. Previous studies and literature on S. douglasi

There are only 14 known studies of the species, of which nine are published. *S. douglasi* was first described by Archer (1979) from four museum specimens that had been collected from the Julia Creek and Richmond area in north-central Queensland between 1911 and 1972. This study focused on the morphology and distribution of this species in comparison to other *Sminthopsis* species. *S. douglasi* was considered extinct until it was rediscovered by Woolley (1992). Woolley's findings extended the range of the species considerably. Similarly, new research of *S. douglasi* published by Kutt (2003) extended the known range of the species further south east of the central parts of Queensland. Two studies (Blacket et al. 2001; Blacket et al. 1999) examined phylogenetic relationships within the *Sminthopsis* genus, based on DNA-sequence analysis. Spencer, Fetcher & Woolley (2003) examined mictosatelite markers in the genome of *S. douglasi*. Five studies focus on the physiology of the species, examining torpor (Muller 1996), growth and development (Beckman 1997), respiration in newborns (Frappell & Mortola 2000), muscles of the pouch (Woolley et al. 2002) and physiology of the intestine (Hume, Smith & Woolley 2000). Only one study of *S. douglasi* focuses on behaviour (Mifsud 1994). That study described nesting and burrowing behaviour, and the role of threat displays in communication. Two ecological studies of *S. douglasi* (Mifsud 1999, 2001) focus on the following topics: i) effectiveness of pitfall and Elliott trapping, ii) the natural habitat of *S. douglasi*, iii) predation on *S. douglasi* by introduced predators and (vi) impact of fire on *S. douglasi* populations. However, very little is known of the behaviour and reproduction of *S.*

douglasi. There are two reasons why studies of *S. douglasi* are so limited. Firstly, the species was only rediscovered thirteen years ago, so its existence has been known for a relatively short period of time. Secondly, *S. douglasi* is an endangered species so access to animals for study purposes has been very restricted.

The family *Dasyuridae* includes a large number of relatively unspecialised predators (51 species in Australia, Strahan 2002). These are divided into 13 genera: *Dasycercus (*mulgara*)*, *Dasykaluta* (kaluta), *Dasyuorides* (kowari), *Dasyurus* (quolls), *Parantechinus* (dibblers), *Pseudantechinus* (pseudantecinuses), *Sarcophilus* (tasmanian devil), *Antechinus* (antechinuses), *Phascogale* (phascogales), *Planigale* (planigales), *Ningaui* (ningauis), *Antechinomys* (kultarr), and *Sminthopsis* (dunnarts; Strahan 2002).

1.3 Ecology of the Dasyuridae

1.3.1 Reproduction

Life history strategy describes the reproductive traits of a species. Lee, Woolley & Braithwaite (1982) reviewed the life history strategies of 30 dasyurid species (not including *S. douglasi*). They identified six strategies distinguished by frequency of female reproduction, season of breeding, age at maturity and timing and duration of reproductive investment by males. *Sminthopsis spp.* were placed into category IV, as they are polyoestrous (undergo oestrus more than once per year), iteroparous (live for more than one reproductive season) and the breeding period is extended but seasonal (winter, spring and summer).

Oestrus cycle in *Sminthopsis spp* varies in length between 23 and33 days dependent on species. Mean oestrus cycle length of 31.1 days has been reported in *S. crassicaudata* (Smith, Bennett & Chesson 1978), 23.3 days in *S. macroura* (Woolley 1990), 26.2 days in *S. larapinta* (Godfrey 1969a), 23.8 days in *S. murina* (Fox & Whitford 1982) and 32.6 days in *S. virginae* (Taplin 1980). Oestrus length (cornified cells present in the urine) lasts 2-9 days, with a mean of 5.2 days in *S. larapinta* (Godfrey 1969a), and 6.3 days in *S. macroura* (Woolley 1990).

Reproduction in *Sminthopsis spp* (Godfrey 1969a;b; McAllan 2003), as in many other dasyurid marsupials (Selwood 1985; Scott 1986; McAllan & Dickman 1986) is timed in order to optimise the chance of successful production of young. Environmental cues trigger physiological and behavioural responses and thereby facilitate the timing of reproduction. The most important cue for the onset of reproduction in dasyurids appears to be photoperiod (Godfrey 1969b; Selwood 1985; Scott 1986; McAllan & Dickman 1986). The onset of the mating period in *Antechinus stuartii* is correlated with the rate of change in photoperiod, rather than with critical photoperiod length (McAllan & Dickman 1986; McAllan, Joss & Firth 1991). Conversely, in *Sminthopsis spp*, increasing photoperiodic length is the most evident cue, as reproductive activity decreases when the photoperiod length decreases after the summer solstice in January (Godfrey 1969b; McAllan & Dickman 1986).

It is possible that factors such as ambient temperature or availability of food resources could also modulate the date of the onset of oestrus in dasyurids. However, these factors do not allow for very precise timing as they may differ from year to year (Scott 1986; Selwood 1985).

Social cues have been found to mediate synchrony of ovulation in female *A. stuartii* (Scott 1986). Isolated females in natural photoperiod ovulated asynchronously whereas isolated females that received pheromonal cues from urine and faeces of other females ovulated in synchrony with them. However, social cues mediating synchrony of ovulation could not control determine the timing of seasonal breeding of *A. stuartii* in the absence of the appropriate environmental cues (Scott 1986).

1.3.2 Daily activity cycle

Nocturnal activity occurs in mammal species for a number of reasons, including predator avoidance and reduction of competition for resources (Ashby 1972; Hall 1980). Dasyurids, including *Sminthopsis spp*, display mainly nocturnal activity (Crowcroft & Godfrey 1968; Ewer 1968; Hall 1980). Captive *S. crassicaudata* show two activity peaks, one at dusk and one at dawn. These activity peaks appear to be associated with the times they are fed. The reminder of the night-time activity consists of bursts of activity interspersed with periods of rest (Ewer 1968). Unlike *S. crassicaudata*, *S. macroura frogatti* did not seem to display a second activity peak at dawn; following the emergence at dusk, there was a concentration of activity in the first 2-4 hours (Crowcroft & Godfrey 1968; O'Reilly, Armstrong & Coleman 1984). The activity then declined to daytime levels, with less activity occurring between 0200 hrs-0600 hrs (O'Reilly, Armstrong & Coleman 1984). This pattern resembles that reported in *Planigale ingrami, P. tenuirostris P. gilesi* and *Dasyuroides byrnei* (Andrew & Settle 1982; Aslin 1974; Braithwaite 1974; Hall 1980).

1.3.3 Torpor

Most carnivorous marsupials are small and, therefore, have a high body surface area to body volume ratio, which may lead to high heat loss when ambient temperatures are low. In addition, many of these species live in environments where the availability of food resources is unpredictable. To conserve energy, many of these species utilise bouts of torpor where they lower their metabolic rate to 10-60% of the basal metabolic rate and consequently lower their energy expenditure (Geiser 2003). Torpor has been observed in about 50% of dasyurids including *S. douglasi* (Geiser 2003; Muller 1996). Torpor usually lasts for several hours, typically commencing just before or after dawn. Torpor can be initiated spontaneously (*S. larapinta*, Godfrey 1968; *S. murina*, Geiser et al. 1984), as a response to food shortage (*S. crassicaudata*, Godfrey 1968), as a consequence of low ambient temperatures (*S. crassicaudata*; Morton 1978a), due to changes in the daylight pattern (photo phase) or as a combination of all of these factors (*S. macroura*, Geiser & Baudinette 1985; *S. crassicaudata*, Holloway & Geiser 1996) . It has also been shown that depth and duration of torpor are strongly influenced by body mass of the animal; the lower the body mass, the lower the minimum body temperature and the longer the torpor duration (Geiser 1988). *S. douglasi* is the largest of the S*minthopsidae* so it would therefore be expected to have lighter and shorter torpor compared with that of smaller *Sminthopsis* species. By studying the effect of food deprivation and temperature on *S. douglasi* in captivity, Muller (1996) revealed that *S. douglasi* became torpid at low ambient temperatures (below 23°C), but only if the animals were unfed. In such cases, torpor would be expected to reduce energy costs when the metabolic demands of euthermy are high and food less abundant, such as during the colder months of the year. Muller (1996) also found that of the *S. douglasi* that became torpid, most did so during the early hours of the morning.

1.3.4 Nesting

The construction of a nest by *Sminthopsis spp.* is driven by the instinct to establish a place to rear the young, and thus often associated with pregnancy (Ewer 1968; Read 1984a). Mifsud (1994) studied the nest building of captive *S. douglasi*. He suggested that nest building is directly related to the reproductive state of the individual. Only female *S. douglasi* build nests. They start constructing a nest when they are in oestrus and continue if they have pouch young. The nests are generally constructed from leaves, grass, shredded paper (in captivity) etc. Mifsud (1994) suggested that the reluctance to build a nest except when expecting young indicates that the species does not have a stable home range. The energy cost of constructing a nest would be unnecessarily high if the animal was continually moving between different locations. However, when rearing young, the female must remain in one location and construct a nest until the young are weaned.

1.3.5 Agonistic behaviour

Agonistic behaviour includes elements of both aggression and submission found in two contexts; sexual competition and resource competition (Croft 2003). The solitary organization of many dasyurids may reduce the frequency of social encounters. Thus, when encounters are staged in captivity or in the field the animals are usually socially intolerant (Croft 2003). Braithwaite (1974) observed that male and female *A. stuartii* behave quite differently with regards to antagonistic behaviours, the males being more aggressive than the females. He also found that the males become increasingly aggressive during the mating season. In contrast, Morton (1978b) and Righetti, Fox & Croft (2000) reported little difference in agonistic behaviour between the sexes of *S. crassicaudata*, *A. stuartii*, *A. swansonii* or *S. murina.*

Ewer (1968) observed that male *S. crassicaudata* would only fight each other when there was an oestrous female present. Aggressive behaviour would cease as soon as the female came out of oestrus. This implies that aggressive behaviour of the males is directed primarily towards claiming an oestrous female and not at securing food or defending a territory. Furthermore, Ewer (1968) and Morton (1978b) found that agonistic behaviour between female *S. crassicaudata* was rarely observed when one of the females was pregnant or cared for young. Fights between a male and a female were limited to periods when the female was in oestrus and were usually initiated by the female attacking the male. Hostile behaviour changed as the animals got older; with females in particular becoming less tolerant towards both males and other females (Ewer 1968).

Van-Dyck (1979) suggested that the aggressive character of *P. maculata* is an indication of “female’s choice” in the biology of this species as well as that of other socially intolerant dasyurids. He argued that only the largest and fittest males would be able to defeat the female’s aggression, which would probably result in selection against smaller and weaker males.

1.3.6 Diet

Dasyurids are opportunistic feeders with arthropods being the main food item (Fox & Whitford 1982; Hall 1980; Morton, Denny & Read 1983; Read 1989). They have a general carnivorous diet that also includes lizards, birds and small mammals. Although dasyurids are primarily carnivorous they include plant material in their diet, especially when insect abundance is low (Blackhall 1980; Fox & Whitford 1982; Strahan 2002).

When fed on a diet of insects containing more than 60% water, *S. crassicaudata and P. maculata* can survive without additional drinking water (Morton 1980). This is possible because of the high water content of their food rather than an adaptation to dry climates. It suggests that feeding on insects (rather than grain, which is the diet of many other desert dwelling mammals) reduces the problem of water conservation (Morton 1980).

1.3.7 Niche separation

The *Dasyuridae* are characterized by an overall lack of specialization (Fox 1982). This may lead to restrictions to species co-existing in the same area (sympatry), because they rely on the same general resources. There are several suggestions as to what separates the different species to make niche-sharing possible.

Sexual dimorphism (different size of males and females) contributes to an expanded niche for a species according to Dickman (1980) and Fox (1982). Body size is also an important factor aiding sympatry between dasyurid species (Dickman 1980; 1988). A marked separation in body size results in the different species focusing on different sized prey (Dickman 1988).

Read (1984b) suggested that mobility is an important factor associated with niche separation between sympatric species. He compared *S. crassicaudata* and *P. gilesi*, which both utilise the habitat of deep cracking soils. The ground surface has greater fluctuations in the abundance of prey, which can be utilized by a highly mobile predator such as *S. crassicaudata*. A less mobile species e.g *P. gilesi* specializes on the microhabitat in soil cracks that provides a more stabile environment with continuous insect abundance.

S. douglasi occur sympatrically with *S. macroura*, *P. tenuirostris, P. gilesi* and *P. ingrami* (Mifsud 1999; pers. obs). *S. douglasi* is distinguished from these other species by its larger size, which may be part of a strategy for co-existing.

1.3.8 Home range and dispersal

Home range is the area over which an animal normally travels in pursuit of its routine activities. Morton (1978b) found that female and male *S. crassicaudata* inhabit large home ranges (movements exceed 500 meters over a period of several days) that overlap those of other individuals. These home ranges are unstable in space and can be described as "drifting home ranges". *S. crassicaudata* does not appear to defend a territory. The only individuals that may become territorial are breeding females, and they probably defend only a small area around the nest.. Males do not seem to be territorial at any time (Morton 1978b). The same pattern was revealed in studies of pygmy-possums (*Cercartetus nanus*) where males had significantly larger short-term home ranges (0.35 ha) than females (0.14) and tended to move over greater distances each night (Bladon, Dickman & Hume 2002). Similarlyly, in *P. gilesi* and *P. tenuirostris* (Read 1984b; 1989), both females and males continually shift home ranges and can travel more than one kilometre in a period of several days. Drifting home ranges were also noted in *S. youngsoni* and *S. hirtipes* (Dickman, Predavec & Downey 1995). Read (1984b) suggested that the ephemeral character of home ranges has important implications for dispersal and social organization of many dasyurid species. For example, it could be a way of avoiding inbreeding (Dobson 1982; Read 1984a; 1984b). However, Mifsud (1999; 2001) found patterns of movement in *S. douglasi* that were different from those identified by Morton (1978b) and Read (1984b; 1989). He suggested that *S. douglasi* is highly mobile but occupies a stable home range, varying in size from 0.25 ha to 7.125 ha. The home ranges of male and female *S. douglasi* overlap those of several other males and females of the same species. This suggests that intra-specific competition is low between individual *S. douglasi*. Mifsud (1999) also observed that mobility was greater in male compared to female *S. douglasi.* This could be a reflection of the male-biased dispersal that has evolved in several mammals as a means of inbreeding avoidance (Cockburn, Scott & Scotts 1985; Dobson 1982).

1.4 Senses and communication

1.4.1 Vision

It was widely believed that nocturnal animals such as dasyurids had relatively poor eyesight and that vision was a less important sense for dasyurids (Russell 1984; Van-Dyck 1979). Ashby's (1972) description of the eye of a typical nocturnal mammal included a large lens and cornea but only rods as sensory cells. This would exclude the ability to see colour, but give a brighter image for any given illumination. However, recent research has shown that the vision of dunnarts and other marsupials is better than previously thought (Arrese et al. 2002; Arrese et al. 2003). Examinations of eyes of possums and dunnarts with micro spectrophotometers revealed that they have at least three types of retinal cones. This provides them with colour vision in the spectra from red to ultra violet. Arrese et al. (2002) suggested that when early placental mammals lost their need for colour vision, marsupials retained it because it was beneficial to be able to distinguish between green-brown tones on the forest floor in their hunt for insects and lizards.

There are several modes of visual communication in dasyurids, involving body postures and flashing colours. An example of such visual communication is the threat posture (Aslin 1974; Russell 1984), where the animal has its mouth open, displaying its teeth and/or holding an erect posture, which makes the lighter ventral surface of the body visible. Exposure of the white throat patch is a gesture of submission in *S. crassicaudata* (Ewer 1968). Hutson (1982) reported that when he dyed the tail of *D. byrnei* black, it reduced fighting behaviour. He suggested that the tail might be used as an effective visual threat signal.

1.4.2 Smell

Olfactory signals are an important mode of communication in dasyurids, whose sense of smell is well developed (Russell 1984; Van-Dyck 1979). Marsupials have extensive areas of olfactory receptor cells and prominent olfactory lobes in the brain, and the vomero-nasal organ is well developed (Croft 1982; Russell 1984). Important sources of odour include urine, faeces, saliva, sweat and secretions from scent glands (specialised cutaneous glands) (Johnson 1973). Scent glands are found to a varying extent in most mammal species. Dasyurids have scent glands on the ears, mouth, lips, chin, sterna, pouch and cloaca (Johnson 1973).

Scent marking is the behaviour by which glandular secretions are deposited on the ground, on objects in the environment or on the animals themselves (Johnson 1973). Scent marking may act as: (i) a substitute for aggression to warn other individuals to stay away from occupied territory, (ii) a sexual attractant or stimulant, sometimes involving the action of pheromones, (iii) a system for labelling the habitat for an animal's own orientation or to maintain a sense of familiarity over the area, (iv) an indicator of individual identity, perhaps including information about sexual status, age, dominance, etc. (v) alarm signals or (vi) kin recognition (Johnson 1973; Croft 1982; Mifsud 1994).

Scent marking is common in the *Dasyuridae*. Individuals of the same species can usually recognize each other by mouth sniffing (*S. crassicaudata*, Ewer 1968; *P. maculata*, Van-Dyck 1979; *S. douglasi*, Misfud 1994). Urination and defecation are used as olfactory signals. Ewer (1968) distinguished "deliberate" from "casual" defecation of *S. crassicaudata*. Similar behaviour appears to be displayed by *P. maculata* (Van-Dyck 1979). Rubbing the face, sternum and cloaca against the ground, objects in the surroundings or against other individuals are other common forms of marking behaviour of dasyurids (Croft 1982; Johnson 1973; Van-Dyck 1979).

The behaviour of dasyurids is influenced by social cues, driven by olfactory signals between individuals. Ewer (1968) discovered that when a male and a female *S. crassicaudata* were housed together, usually it was only the male who would scent mark in response to alien objects and odours. The female would only scent mark if the stimulation to do so was unusually strong, e.g. if she was carrying pouch young.

Fadem (1989) and Fadem & Rayve (1985) confirmed in studies of captive short-tailed opossums *Monodelphis domestica*, a non-dasyurid species, that oestrus is influenced by social factors. Exposure to male pheromones activated oestrus in females, both when the female and male were housed together and when single females were exposed to male scent marks. Oestrus was not activated in females housed singularly without scent cues (Fadem 1989). Females housed together with males showed more days of cornified cell proliferation than did females housed alone. The oestrous cycle also occurred in synchrony between females (Fadem 1989; Fadem & Rayve 1985).

1.4.3 Vocalization

Many different messages appear to be delivered by vocalizations. Vocalization provides a clear message that travels quickly over long distances (Croft 1982). A repertoire of at least five calls has been characterised in the dasyurids (Croft 1982; Ewer 1968; Fox 1982; Fox & Whitford 1982; Van-Dyck 1979). Most of these are described as "rhitt" "chee", "hiss", "huff" "zitt" or "click" calls that may be repeated and are of varying intensity (Aslin 1974; Braithwaite 1974; Read 1984a; Taplin 1980; Van-Dyck 1979). A sonographic analysis of the call repertoire of *S. crassicaudata* (Bishop et al. 1995) did not find any ultra sonic calls outside of the human audible range.

The vocal repertoires observed in *S. douglasi* include "hiss" sounds associated with agonistic behaviour, followed by tendencies to attack the opponent. "Chee“ vocalisations occur in response to overt aggression and reflect tendencies to flee (Mifsud 1994). Additional sounds with unknown purpose have been observed (Bjursell pers. Obs.). Van-Dyck (1979) described the vocalization repertoire of *P. maculata.* This includes threat calls, possession calls that were repeated when an individual retreated with food, an appeasement call uttered by a male being attacked by a female, and a mate-attracting call. Van-Dyck (1979) suggested that a mate attracting call was a consequence of a species adapting to a solitary life style. Male and female mate-attracting calls have been identified in several other dasyurid species; *A. laniger* (Happold 1971), *S. virginae* (Taplin 1980), *P. gilesi* and *P. tenuirostris* (Read 1984a).

1.5 Ecology of S. douglasi

1.5.1 Habitat

There are 19 species of dunnarts in Australia, but only *S. douglasi* is restricted to Queensland. *S. douglasi* is a habitat specialist, utilising soil cracks in the ashy and stony cracking soil of mitchell grass plains (Woolley 1992; Crowther& Blacket 2003). The soil cracks provide shelter from predators, extreme temperatures and fire (Mifsud 1999). *S. douglasi* can flatten itself very effectively, enabling it to get down into soil cracks (Lundie-Jenkins & Payne 2000). The area where *S. douglasi* occurs generally has hot, wet summers with temperatures exceeding 35°C and cool dry winters. Rainfall is highly unpredictable, but permanent water is present in dams, rivers and creeks throughout the area (Orr & Holmes 1984). During the summer rain period, the ground swells and the cracks close partially. However, following the rain, a growth spurt of grass occurs that provides *S. douglasi* with alternative shelter (Lundie-Jenkins & Payne 2000; Orr & Holmes 1984).

1.5.2 Morphology

Adult weight of *S. douglasi* is 40-60 g for females, and 50-70 g for males. This makes it the largest member of the *Sminthopsis* genus. The fur is light brown and speckled grey with a white belly (Woolley 2002). This coloration camouflages the animals in their natural environment, and has probably evolved as a response to predation (Mifsud 1994). The tail is 120-130 mm in adult males and fattened at the base. *S. douglasi* has a striped face, which makes it difficult to distinguish from the stripe-faced dunnart (*S. macroura*). *S. douglasi* is also morphologically similar to the red-cheeked dunnart (*S. virginae*), from which it can be distinguished by the dark hairs at the tip of its tail and the dark rings around its eyes (Woolley 2002). Like all Dasyurids, *S douglasi* has four pairs of sharp incisors in the upper jaw and three similar incisor pairs in the lower jaw. Canine teeth are well developed and pre-molars and molars are sharp and serrated. This is consistent with an insectivorous diet. The snout of *S. douglasi* is slightly elongated and the four feet are of similar length (Strahan 2002).

1.5.3 Reproduction

S. douglasi is polyoestrous (go through oestrus more than once per year) and breeds between June and February (Beckman 1997). The females have eight teats and can rear up to eight young in a litter. The species can rear two litters per season. Females reach sexual maturity after 17-27 weeks and the males after 28-31 weeks (Beckman 1997). This difference in time to attain sexual maturity may be an important way to prevent inbreeding in the species, as the females mate before their male litter mates are sexually mature (Woolley 2002).

1.5.4 Conservation status

Dasyurid marsupials are distributed throughout the terrestrial habitats of Australia, but since European settlement they have suffered population declines and extinctions. Seven sminthopsis species are classified as vulnerable, endangered, critically endangered or data deficient on the IUCN Red List of Threatened Animals (Wilson, Dickman & Fletcher 2003). Species that occupy few habitats are of greater risk of extinction. *S. douglasi*, is confined to one habitat type (Dickman et al. 2001; Wilson, et al. 2003).

S. douglasi is listed as Endangered on the IUCN Red List of Threatened Animals (IUCN 1996). Climatic factors, current land use and introduced predators have contributed to its current status as endangered. An investigation of the stomach contents of feral cats (*Felis catus*) showed that they are a major predator of *S. douglasi* in its natural habitat (Mifsud 1999). Mifsud (1999) suggested that feral cats could be responsible for local extinctions of *S. douglasi*. Barn owls (*Tyto alba*) have been observed to take small numbers of dunnarts, but this probably does not have a severe impact on *S. douglasi* populations (Mifsud 1999). There are no reports in the literature of foxes (*Vulpes vulpes*), dingoes (*Canis lupus dingo*) or snakes taking dunnarts. Another factor that may have contributed to the decline of *S. douglasi* was the introduction of prickly acacia (*Acacia nilotica*). This weed species has spread over seven million hectares of Mitchell grass downs and altered the normal habitat structure so that it is no longer suitable habitat for *S. douglsai* (Lundie-Jenkins & Payne 2000).

Queensland Parks and Wildlife Service (QPWS) initiated a recovery plan for *S. douglasi* (Lundie-Jenkins & Payne 2000). The plan (Recovery plan for the Julia Creek dunnart (*Sminthopsis douglasi*) 2000-2004; http://www.epa.qld.gov.au/publications?id=176.) includes protection and restoration of suitable habitat; management of predators; further investigation of distribution and ecology, as well as captive breeding programs at David Fleay Wildlife Park (Fleay), Burleigh Heads (Lundie-Jenkins & Payne 2000).

1.5.5 Captive breeding

Individual *S. douglasi* and other *Sminthopsis* species can be very aggressive towards each other (Mifsud 1994; Righetti, Fox & Croft 2000; Taplin 1980) and it is therefore appropriate to keep them caged individually. When the females are in oestrus, they are paired with a suitable (unrelated) male so that mating can occur. Not every mating is successful. The current method of determining the reproductive status of female and male *S. douglasi* (described by Godfrey 1969a) is to collect a drop of urine and examine it under a microscope. If the female is in oestrus, cornified cells will be present in the urine. Sperm can be seen in the urine of sexually mature males during the reproductive period. Both cornified cells and sperm can be seen through a microscope at 100x magnification. This method is reliable but it involves handling individual *S. douglasi* and is therefore regarded as invasive. *S. douglasi* does not respond well to handling, and the animals do not seem to get accustomed to handling after a period in captivity (Bjursell, pers. Obs.). Thus, daily urine sampling will cause some stress to the animals. This method is also labour intensive, especially as the populations grow larger. Because of the short duration of the oestrous (3-5 days, Bjursell pers. Obs.) it is easy to miss oestrous if the dunnarts are not sampled every day. Another method of identifying oestrus in mammals is to determine the concentration of metabolites of hormones (e.g. oestradiol and progestogen) in faeces. Oestrous has previously been identified by this method in the koala (*Phascolarctos cinereus*), chuditch (D*asyurus geoffreii)*, black rhinoceros (*Diceros bicornis minor*), common wombat (*Vombatus ursinus*) and southern hairy-nosed wombat (*Lasihorhinus latifrons*) (Garnier, Holt & Watson 2002; Johnston et al. 2000; Paris et al. 2002; Stead-Richardson et al. 2001 respectively). While this technique is a non-invasive method of identifying oestrus, it is more expensive and time consuming. The delay involved in obtaining the results of the analyses may also render this method impractical in some situations.

1.5.6 Behavioural signs of oestrus

Behavioural signs that may give an indication of reproductive state include vocal and olfactory signals as well as changes in activity and aggressive behaviour. For example, at the onset of breeding activity, both males and females of some dasyurid species make characteristic “mate attracting” calls (*S. murina,* Fox & Whitford 1982; *P. gilesi and P. tenuirostris*, Read 1984a; *S. virginiae*, Taplin 1980; *P. maculata*,Van-Dyck 1979). Olfactory signals, in particular cloacal marking and sniffing of the mouth and cloacal region also seem to play an important role in the reproductive behaviour of the dasyurids (*A. stuartii*, Braithwaite 1974; *S. crassicaudata*, Ewer 1968; *Monodelphis domestica*, Fadem 1989; Fadem & Rayve 1985; Johnson 1973; *P. gilesi and P. tenuirostris*, Read 1984a). Males appear to display more interest in the females during oestrus, sniffing the cloaca of the female and making attempts to mount (*Dasyurus Geofferii,* Stead-Richardson et al. 2001; *P. maculata*, Van-Dyck 1979). Previous studies have reported behavioural changes in females as they enter oestrus, including increased nocturnal activity (*Ningaui spp*., Fanning 1982; *P. maculata*, Van-Dyck

1979), construction of a nest (Mifsud 1994) and increases or decreases in aggressive behaviour towards other females and males (*S. crassicaudata*, Ewer 1968; *D. byrnei*, Ganslosser & Meissner 1984; *S. virginiae*, Taplin 1980; *P. maculata*, Van-Dyck 1979). Onset of oestrus in *D. byrnei* can be readily detected by noting significant behavioural changes in females and males (Ganslosser & Meissner 1984). Female *D. byrnei* do not tolerate the male (although they will tolerate other females) except when they are in oestrus. In addition, the frequency of urinary marking by both female and male *D. byrnei* increases dramatically when the females experience oestrus (Ganslosser & Meissner 1984).

Physiological signs that may be used to identify oestrus, in addition to the presence of cornified cells in urine, are changes in weight and appetite. Woolley (1984) observed that the appearance of cornified cells in urine of *A. laniger* was associated with a temporary but sharp increase in body weight followed by a sharp decrease in body weight.

A second less marked increase in body weight usually commences at about the time cornified cells are no longer present in the urine. Similarly, a rapid increase in body weight in combination with oestrus has also been observed in *S. macroura* (Woolley 1990) and *D. byrnei* (Close 1983). Swelling of the cloaca has been observed during oestrus (*P. gilesi and P. tenuirostris,* Read 1984a; *D. Geofferii,* Stead-Richardson et al. 2001; *P. maculata,*. Van-Dyck 1979). There are some indications that pouch appearance may vary during the oestrous cycle, the pouch becoming slightly red in colour and becoming swollen during oestrous (*P. gilesi and P. tenuirostris*, Read 1984a; *S. virginiae*, Taplin 1980). However, pouch condition is not a reliable sign of the onset of oestrus in *S. crassicaudata* according to Godfrey & Crowcroft (1971).

1.5.7 Alternative method for determining oestrus

The first documentary evidence that female mammals display a predictable change in behaviour when in oestrus was published by Wang (1923) and Slonaker (1924) who reported that the degree of physical activity of female white rats (*Rattus norvegicus*) was closely correlated with the stage of the oestrous cycle. They found that running activity was significantly elevated when rats were in oestrus. Farris (1944) supported this finding in the rat. He also reported that women showed elevated physical activity on the day of ovulation. Altman (1941) reported that sows in oestrus (*Sus scrofa domesticus*) exhibited twice the physical activity when compared with other stages of the oestrus cycle. The relationship between physical activity and oestrus was also established in dairy cows (*Bos taurus*) by Farris (1944), who reported a significant increase of the physical activity in cows in oestrus compared to non-oestrus. Despite the success in placental mammals, there are no studies to date that have tried to link behaviour to oestrous state in dasyurids or other marsupial species. However, because the behavioural oestrus of some species can be observed, this can potentially be used instead of collecting urine samples (which provides the information of oestrus state) to determine oestrous (Jackson 3003).

1.5.8 Summary of this study

In Chapter two, I tested the hypothesis that there are measurable characters in the behaviour of female *Sminthopsis douglasi* that change from when the females are in the state of oestrous compared from when they are non oestrus. If this is the case, what are these behavioural characters, and how long do the females need to be observed for in order to identify the reproductive state reliably?

In chapter three, I tested whether the behavioural patterns in oestrus and non-oestrus females are the same, regardless of the social context, i.e. when the female is accompanied by another female, a male or housed solitarily.

Finally, in chapter four, I tested whether the changes in behaviour can be measured with an automated procedure rather than direct observations. This would possibly reduce the time required to identify reproductive state based on behaviour, which would be highly desirable in a management situation.

A method to identify specific behaviours of *S. douglasi* that can be correlated with oestrus would improve our understanding of the reproductive biology and behaviour of *S. douglasi*. The ability to detect oestrus by merely observing behaviour would be a non-invasive way to enhance the success of breeding the species in captivity, particularly if the behaviours are readily detectable in a brief period of observation.

This study initially included field observations of *S.douglasi*, in Bladensburg National Park, Winton, Queensland. *S. Douglasi* has been abundant in this area previously (Misfud 2001). Two field trials were conducted, including 2694 trap nights in July 2003 and March 2004. However, this showed a very low abundance of *S. douglasi*. Because of the low number of *S. douglasi*, the field surveys were not further included this study. An outline of the field studies is presented in Appendix 1.

Chapter 2

Study 1 - Development of a system of behavioural observation to detect reproductive status

2.1. Introduction

Given the difficulties associated with husbandry of this species the primary aim of the current research was to develop a method for determining the oestrous state of *S. douglasi* that minimised the invasive aspects of handling and acquiring urine samples from the female. This was achieved through behavioural observation procedures, which were designed to determine if there were any measurable differences in the behaviour of female *S. douglasi* in the oestrus and non oestrus states. These relied on the development of a method of observing and measuring behaviour and selecting specific behaviours; in particular combinations, that would best discriminate between the two reproductive states (oestrus / non-oestrus). This in turn required selecting appropriate individuals to observe (females, males or both). Another aim of this study was to create a model that would identify oestrus with a minimum of observation time. These goals formed the basis of Study 1.

2.2. Methods

2.2.1 The captive population

The original captive population of *S. douglasi* was first established by Dr. Pat Woolley at La Trobe University in 1992 and initially consisted of seven wild-caught animals (three females and four males). Animals from that population were subsequently relocated to David Fleay Wildlife Park (DFWP), Burleigh Heads, Queensland in 1999 where the breeding program of *S. douglasi* was continued. The first part of this study (pilot study and targeting initial behaviours; section 2.2.5) was conducted at DFWP. In 2004, ten individuals from the DFWP population were transferred to the University of Southern Queensland for the remaining parts of this study.

All studies were approved by the University of Southern Queensland Animal Ethics Committee and Queensland Environmental Protection Agency.

2.2.2 Housing

Husbandry and handling of *S. douglasi* were in accordance with guidelines for the management of Australian carnivorous marsupials outlined by

(Woolley 1982) and Jackson (2003). The dunnarts were housed in enclosures 90x52x57cm made from a non-porous material with transparent perspex front. Each pair of monitor cages (Figure 1) were separated in the middle by a 5mm wire mesh with the female to the right and the male on the left side. Selection criteria for the study were that all *S. douglasi* had to be of reproductive age (1-2 years) and pairs of males and females in the enclosures were not directly related (siblings or parent – offspring). The dunnarts could see, hear and smell each other, but they had limited scope for physical contact. Similarly-structured enclosures have been used in previous behavioural studies of small dasyurids (Woolley 1982; Fadem & Rayve 1985; Carnio 1993; Bishop et al.1995; Righetti Fox & Croft 2000; Jackson 2003).

The floor of each enclosure was covered with sand to a depth of approximately 1cm. Each individual *S. douglasi* had a wooden or plastic nest box 10x10x10cm with shredded paper provided as nesting material. Each animal was provided with an exercise wheel (17cm diameter), small rocks, cardboard tubes and pieces of bark for habitat enrichment. Each animal was fed daily between 3 and 4 pm (Eastern Standard Time) with 10 meal worms (*Tenebrio molitor*) and 8-12g of meat mix, containing beef heart, beef liver, sheep brain, egg, dry cat food (Eucanuba) and calcium carbonate (Woolley 1982). The meat mix was frozen for at least four weeks prior to feeding to minimise the risk of spreading parasites such as *Toxoplasma gondii* (causes toxoplasmosis) to the dunnart colony. Occasionally the dunnarts were fed crickets (Orthoptera), cat biscuits (Eucanuba) and egg custard. Water was available *ad libitum.*

Timing of reproduction of captive animals may be an artefact of the lighting regime employed (Selwood 1985; Scott 1986; McAllan, Joss & Firth 1991). Thus, the room where the animals were housed was kept on a normal daylight cycle by access to natural daylight through uncovered windows. The room was kept at 22 ± 3°C with a reverse-cycle air conditioner. Within this temperature range the dunnarts would not be required to utilise torpor unless they were deprived of food (Muller 1996).

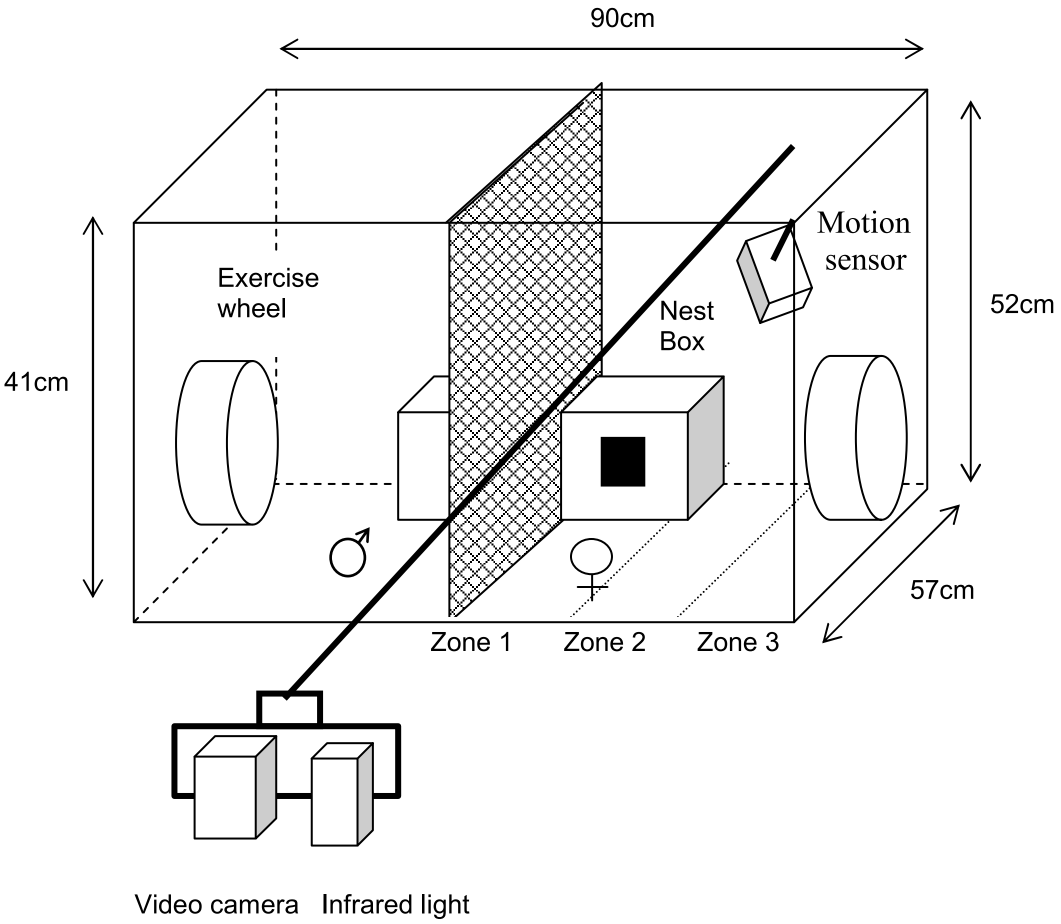


Figure 1. Monitor enclosure for *S. douglasi*. The cages were divided in the middle by a 5x5 mm wire mesh with the female to the right and the male on the left side. This limited contact between animals. The floor was covered with sand and each individual had a nest box and an exercise wheel. An infrared video camera, a motion sensor and infrared light emitting diodes were in place to record the animals' behaviour.

2.2.3 Urine sampling, examination and determination of oestrous state

Each female was weighed, examined for signs of illness or injury and urine samples were collected before feeding, 2-3 times per week in the initial part of the study, and thereafter daily. Observations included coat condition, state of the pouch (red, swollen and/or badly groomed), food consumption (food leftovers, recorded daily to the nearest 0.5g) and possible discharge from eyes, ears, mouth or cloaca. Body weight was measured to 0.5g and used as a general indicator of health condition. Sampling involved removing the animal from its enclosure, placing it in a cloth bag and collecting several drops of urine directly from the cloacal opening on to a microscope slide. Urine samples from female *S. douglasi* were examined for the presence of cornified cells, which are readily abundant during oestrus and can be detected at 100x magnification without staining (Godfrey 1969a; Selwood 1982, 1985). The "on-off" presentation of cornified cells is not strictly correct for most dasyurids. Numbers of cornified cells increase and then decrease (Godfery1969a; McAllan, Joss & Firth 1991). However, for the purpose of this study, only oestrus / non oestrus i.e. the presence or absence of cornified cells was used. Male S. douglasi were subjected to similar general health examinations approximately once per week, when urine samples from males were examined for the presence of sperm.

2.2.4 Recording methods

The sampling method used for acquisition of behavioural data was focal sampling. Focal sampling involves observing one individual for a specified amount of time and recording all instances of targeted behaviour (Altman 1974; Martin & Bateson 1993). To eliminate issues of inter-rater reliability (sample error introduced by using different observers), the same person recorded all observations. Behaviour was observed for two nights when a female was in physiological oestrus (cornified cells present in the urine) and two nights when the same animal was non-oestrus. Behaviour was analysed in three females (n=3, totalling 12 nights; 96hours). The mean frequency of behaviours was calculated as the total number of occurrences of the behaviour per minute the female was active during the night.

Video recording was selected as the most appropriate method to monitor the dunnarts. This was because the animals are nocturnal and spend long periods of time in their nest boxes in between periods of activity throughout the night. Direct observations covering the entire time period would have been impractical. Furthermore, activity of *S. douglasi* sometimes occurs at a frenetic pace. Many incidences of behaviour may therefore have been overlooked by extended direct observation. Video recording also provides a permanent record that can be reviewed if necessary. The video cameras were not configured for sound and only recorded visual information. Accordingly vocalisations were not targeted as behaviours for study.

A video camera (Monochrome CCD) was arranged in front of the cages (Figure 1). The entire enclosure except the far front corner of the left (male) side was in the field of view of the camera. The camera was connected to a motion sensor (Safe House AEI PIR Intrusion Detector) fixed in the top right corner of the cage. This was triggered by movements of the female and some movement of the male. Recording paused if no movement had been detected for three minutes. An infrared array of light-emitting diodes was arranged next to each camera as a source of illumination. This illumination is unlikely to have caused any disturbance to the animals, as dunnarts cannot see the infrared spectrum (Arrese et al. 2003).

The recording spanned the entire duration of the dunnart’s activity to a maximum of eight hours. All observations were obtained during the same period of the day, starting just after feeding. The timing of these observations may have a potential impact on the generalisation of the current findings to behavioural observations conducted at other times.

2.2.5 Targeting initial behaviours

A pilot study was conducted over a five-day period, during which preliminary observations were recorded and initial questions formulated. The pilot study provided a basis for the development of hypotheses and methods of measurement. The choice of behaviours that were initially included in the investigation was based on anecdotal evidence about this species and findings from previous studies of related species.

Only the behaviour of the female *S. douglasi* was recorded, as the behaviour of the female is the focus of this study. The male essentially functioned as a stimulant, since the presence of a male has been shown to trigger some reproductive behaviour in the female of some species (Chicoteau et al. 1989; Fadem 1989; Duchens et al. 1995; Pycock et al. 1995). It is possible that the behaviour of the males in proximity to females changes significantly during female oestrus compared to non oestrus. However, the behavior of the male is outside the scope of this study. The full recording over a night (up to a maximum of eight hours) of the activity of the female was analysed. This was to target specific behaviours, or frequency of specific behaviours, which were likely to become apparent as significant indicators of reproductive state. The female (right) side of the enclosure was divided into three zones of equal size (each approximately 15cm wide): close to the mesh divider, intermediate and away from the wire-mesh divider (see Figure 1). These zones were loosely demarcated by the presence of key objects in each zone. For example, zone 1 contained the entrance to the nest box, while zone 3 contained the exercise wheel. Additionally, two other locations were recognised, on top of and inside the nest box. These permitted quantification of the female's location and duration in the enclosure, and facilitated measurement of activity by assessment of the frequency with which the female moved between the different zones of the enclosure. Due to the fixed location of the camera, the arbitrary divisions that demarcate the zones did not change. However, exact determination of the boundary between divisions was not logistically possible. In this respect, the primary role of zone 2 is that it falls in-between zones 1 and 3. While an observer may be uncertain as to whether or not the female currently resides in zone 1 or zone 2, or zone 2 or zone 3 when she is close to their respective boundaries, the distinction between zone 1 and zone 3 is always clear.

After a preliminary observation period, the frequencies of selected behaviours (see section 2.3.2) were examined. Particular emphasis was placed on eliminating behaviours that occurred with such low frequency that they were unlikely to be observed in a practical observation period. The objective was to devise a method to reliably predict oestrus by monitoring the behaviour of the female for a relatively short time span. Thus, for the purposes of this study, behaviours that occur rarely are not logistically viable, regardless of whether they occur at a significantly different rate during oestrus or not. For example, it is possible that a female *S. douglasi* may groom herself twice during an eight hour period when she is anoestrous, and groom herself ten times during the same time period in oestrous. Grooming is then likely to occur at a significantly higher frequency in oestrous. However, grooming only occurs 1.25 times per hour on average even when the female is in oestrous. If 60 minutes of behaviour were observed and only one occurrence of grooming was recorded, it would be inadvisable to assign the reproductive state of that female on the basis of this one observation. Conversely, if the female *S. douglasi* groomed herself on average 25 times per hour when anoestrus and 125 times per hour when in oestrus, then this would be a more robust behaviour to use for determination of oestrus. As an arbitrary criterion, only those behaviours that occurred with a mean frequency of five or more times per hour (See section 2.3.2) were included in subsequent analyses.

2.2.6. Statistical analysis

Changes in mean body weight and food consumption (mean weight of food leftovers) during oestrus compared to non-oestrus for four females during five months (July-November 2004) was analysed with two-tailed t-tests (Zar 1999) using Microsoft Excel 2003. Frequencies, expressed as mean occurrences of selected behaviours per minute for each animal, along with the standard deviations, were collated and summarised using Microsoft Excel 2003. To determine the effect size of each of the behaviours under examination, Cohen's D (Cohen 1988) were calculated in order to obtain a quantitative measurement of the "treatment effect", oestrus state being seen as "treatment". Cohen (1988) outlined threshold values for effect sizes (ES): 0.2 = small, 0.5 = medium, and 0.8 = large.

Pearson correlations were calculated in order to reveal correlation between the observed behaviours. If behaviours are highly related, predictive accuracy is overestimated due to the inter-relationships amongst the variables in a regression equation. For this reason, a discriminant function analysis (DFA) with stepwise exclusion (Hotelling 1935, Huberty 1994) was conducted using SPSS 12.0 to determine which combination of variables would contribute uniquely and account for the greatest amount of variance in predicting female oestrus state. Discriminant function analysis also generates the canonical coefficient square of the function (R^2_c, Hotelling 1935). This is a goodness-of-fit statistic that describes how much of the variation in the dependent variable (reproductive state) that is explained by the independent variables. R^2_c has a range between zero and one. The larger the R^2_c, the better the independent variables are as predictors of the dependent variable.

2.2.7 Fail Safe N

The robustness of the effects observed is always of concern in studies that utilise small sample sizes (Zar 1999). Therefore, concern remains as to whether observations of a larger number of animals would have generated non-significant results. This issue can be addressed through the computation of the Fail safe N (Rosenthal 1979; Hedges & Olkin 1985). The fail safe N indicates the number of studies that would be required to reduce the effect size observed in a particular study to a non-significant value.

$$\text{Fail Safe N: } k_0 = k(r_1 - r_2)/r_2$$

Where:

k_0 = The number of studies needed to reduce the mean effect sizes to a negligible magnitude.

k= the number of studies in the current study (one, as this is the only known study).

r_1= the mean effect size (1.42 for "zone 3" and –0.71 for "in nest box" in this study; Table 1)

r_2= the proposed effect size that would be of negligible magnitude, which was set at 0.1 (Cohen 1988).

2.2.8 Observation time and accuracy of the function

The discriminant function analysis is based upon data derived from three females and its accuracy may have come from the large number of observations made for long periods of time over extensive recording periods (up to eight hours per night for twelve nights). However, the true test of the usefulness of this model is the frequency with which it accurately identifies the reproductive state of individual females from restricted observation periods. It is not practical in an animal husbandry situation to use a method where several hours of behaviour must be observed in order to reliably detect reproductive state of individual *S. douglasi*. A method that is to be incorporated in management procedures needs to be brief enough to be logistically viable as an observation period but also long enough to ensure the likelihood of observing each of the target behaviours. In order to determine the length of the observation period required to reliably establish reproductive state, analysis frequencies were determined based upon 5-minute recording periods. Data from 94 random five-minute periods were selected from the data set and tested with the model generated in the discriminant function analysis. Starting with one 5-minute observation period, the accuracy of the function was investigated as additional 5-minute periods were added. Subsequently, 94 1x5-minute periods, 47 2x5-minute periods and 31 3x5-minute periods were tested.

The accuracy of the function can be described in terms of:

1. The Positive predictive power (PPP) - the probability that a female is in oestrus (according to presence of cornified cells in the urine), given that she was identified as oestrus using the equation.
2. The Negative predictive power (NPP) - the probability of a female not being in oestrus when the equation produces a non-oestrus score.
3. The Overall predictive power (OPP) reflects the combination of both PPP and NPP.

2.2.9 Cross-validation of the discriminant function

A sub-sample of six females and four males from the DFWP population were relocated to the University of Southern Queensland (USQ) in 2004 for the purposes of conducting the rest of the study. Housing conditions were designed to resemble as much as possible the enclosures in which the animals had dwelled at DFWP (see section 2.2.2). Urine sampling and oestrous determination was conducted as previously described (see section 2.2.3). However, in at USQ, urine was sampled daily instead of 2-3 times per week as done previously. Aside from more frequent urine sampling, methods employed in all studies to observe and record behaviour were identical.

The accuracy of any discriminant function would be greatest when evaluated with the individuals from which it was derived. To examine the potential to generalise this equation to other females of the species and to evaluate the degree of shrinkage in the predictive accuracy, the discriminant function must be cross-validated against a different sample. To verify the accuracy of the equation, a new sample of four female *S. douglasi* were observed for two random five-minute periods under identical conditions to those used when developing the model. Observations were carried out during a six-month period; June – November 2004, and included 20 oestrous and 24 non-oestrous periods in total.

2.3 Results

2.3.1 Timing, body weight and food consumption during oestrus

Data of reproductive state, weight and food consumption (leftover food) is presented in Appendix 2. Oestrus lasted 4-7 days; average five days, with intervals of 10-21 days; average 18.1 days between oestrous once the reproductive period started and cornified cells were first seen in the urine. There was no significant difference in mean body weight of oestrus females compared to non-oestrus females (t-test, df=3, p>0.05). Neither was there any significant difference in mean weight of food consumption (left-over food) between oestrus and non-oestrus females (t-test, df=3, p>0.05).

2.3.2 Targeting initial behaviours

The following behaviours were initially targeted. These were chosen because of the perceived relevance of these behaviours to the animal, and the ease with which a human observer could detect them:

i) Moving between different zones of the enclosure. The female readily moved across and between these zones.

ii) Standing. The animal was standing on it's hind legs and stretched to an upright posture. This behaviour appeared to be associated with exploratory behaviour and sniffing.

iii) Grooming. Grooming was displayed throughout the period of activity. This was displayed either by standing on three legs and scratching the body with the hind foot, or by sitting in the bipedal rounded position (Ewer 1968) and licking the fur directly or licking the paws and rubbing them over the mouth and head.

iv) Eating and drinking. The animals usually consumed all of their food in a short time soon after emerging from the nest boxes in the evening. Typically they were sitting in the bipedal posture holding the food item in one or both hands. Drinking was observed on very few occasions.

v) Exercise. The animals frequently used the exercise wheels. A running session lasted from several seconds to several minutes. Exercise was operationally defined as occurring when the animal had all four feet in the exercise wheel (even if the animal was not running, although this was rarely the case). The exercise session was terminated when the animal left the exercise wheel.

vi) No activity. When the animals were in their nest boxes or alternative shelter they could not be monitored, thus this was classified as no activity. The animals always slept under some kind of shelter. Usually this was the nest box, but they also slept behind the exercise wheel or in the cardboard tube. Characteristically their emergence from the shelter after long periods of absence was followed by a stretch and a yawn, suggesting that they had been sleeping. However, it is possible that they also engaged in other activities inside the nest box, such as grooming.

vii) Encounters. Sometimes both the female and the male approached the dividing mesh between their cages at the same time and sniffed each other, usually front to front. After a brief period of time, usually several seconds, one of the animals would turn away from the other. Sometimes the other individual tried to follow. No aggressive behaviour was observed during these encounters.

viii) Climbing. The animals would regularly climb up the wire partitioning and across the cage top.

ix) Sitting on top of the nest box. The animals frequently positioned themselves on top of objects in the enclosures, in particular the nest box.

x) Running through the tube. A tube of cardboard was provided for alternative shelter and habitat enrichment. The animals ran through this in both directions between different parts of the cage.

xi) Marking. Generally the animals defecated randomly throughout the enclosures with a slight preference for the sides of the cage. When a new object was introduced into a cage, the animal would examine it by sniffing and mark it by defecation.

xii) Digging. Occasionally the animals dug in the sand under objects in the cage. This may have been to catch mealworms that had buried themselves under the surface of the sand.

xiii) Other. This category was included to permit the observer to note any unanticipated or particularly interesting behaviours not previously defined. Interestingly, few behaviours noted in other dasyurid species such as sand bathing and shaking (Aslin 1974; Ewer 1968) were observed in *S. douglasi.* Neither was any extensive nest building observed.

Following the procedure where low-frequency behaviours were excluded, the following ten of the original thirteen behaviours were retained in the protocol:

- *i)* Moving between different zones of the enclosure (zone 1, zone 2 and zone 3; Figure 1).
- *ii)* Entering the nest box
- *iii)* Standing posture
- *iv)* Grooming
- *v)* Eating
- *vi)* Using the exercise wheel
- *vii)* Female-male encounters
- *viii)* Climbing
- *ix)* Sitting on the roof of the nest box
- *x)* Running through the tube

2.3.3 Statistical analysis

The frequencies expressed as mean occurrences of selected behaviours per minute along with the standard deviations of the selected behaviours are presented in Table 1.

To determine the effect size, Cohen's D (Cohen 1988) were calculated (Table 1). The largest effect size (ES) i.e. Cohen's D in this data set (Table 1) is 1.42. This effect size was obtained for the frequency with which the female enters zone 3 (Figure 1) and the value obtained is well above what would be required by Cohen (1988) to be rated as large (0.8). Frequency of entering the nest box was the behaviour that generated the highest negative effect size (Cohen's D = -0.712; Table 1), indicating that the frequency of this behaviour decreased when the female was in oestrus.

Calculated values of Pearson correlations in Table 2 indicate that there is a considerable amount of correlation between several of the observed behaviours. This introduces the problem of multicollinearity. Some behaviours are highly related, so the predictive accuracy is overestimated due to the inter-relationships amongst the variables. However, the discriminant function analysis (DFA) with stepwise exclusion (Hotelling 1935; Huberty 1994) selected which combination of variables would contribute uniquely and account for the greatest amount of variance in predicting female oestrus. Of the twelve behaviours utilised in the analysis to predict oestrus state, only two remained after stepwise exclusion had been performed; i.e. only two behaviours accounted for a significant amount of variance and did not intercorrelate significantly. These two behaviours were frequency of movement into zone 3 and number of times entering the nest box. The equation generated by the DFA (summarised in Figure 2 below) generates a numerical "activity score"; AS, that in turn may be used to identify reproductive state. "Zone 3" indicates the mean number of times the female entered zone 3 per minute and has a coefficient of 1.708 (calculated through DFA). Thus, for every occurrence of the female entering zone 3, 1.708 is added to the activity score AS. "In nest box" indicates the number of times the female entered the nest box per minute and has a coefficient of –4.434. Accordingly, for every instance that the female enters the nest box during the observation period, 4.434 is removed from the activity score. The function calculated by the DFA has a constant of –2.089, which constitute the activity score in the instance that none of the two behaviours occur during the observation period.

AS = 1.708 x zone 3 – 4.434 x in nest box – 2.089
If AS is positive ($AS>0$) then predict oestrus
If AS is negative or equal to zero ($AS\leq0$) then predict non-oestrus.

Figure 2. Equation to establish the reproductive state of female *S. douglasi* generated by a discriminant function analysis based on behavioural observations of three females over twelve nights.

The canonical coefficient square (R^2_c, Hotelling 1935) for the discriminant function (Figure 2) is 0.759. This means that almost 76% of the variation in behaviour between the oestrous and a non-oestrous state is explained by the zone 3 and in nest box variables.

Table 1. Frequency Means (occurrence per minute), Standard Deviations and Effect Sizes of behavioural observations of three female *S. douglasi* in oestrus compared to non-oestrus over twelve nights. Numbers 19, 25 and 26 refers to individual female *S. douglasi*. o1= first oestrous period, o2= second oestrous period, n1=first non-oestrous period, n2= second oestrous period.

Behaviour	**Female**	**19o1**	**19o2**	**19n1**	**19n2**	**25o1**	**25o2**	**25n1**	**25n2**	**26o1**	**26o2**	**26n1**	**26n2**	**Mean Oestrus**	**Mean Non-oestrus**	**Standard deviation**	**Cohen's D**
Zone 3		2.31	2.59	0.90	1.60	3.16	3.29	1.05	1.86	1.64	3.59	2.22	0.20	2.76	1.30	1.03	1.42
Exercice		2.09	2.29	1.23	1.39	2.69	3.12	0.94	1.79	1.18	1.65	1.63	0.08	2.17	1.18	0.81	1.22
Encounters		0.31	0.77	0.26	0.33	0.64	1.21	0.08	0.24	0.08	0.38	0.15	0.06	0.57	0.19	0.34	1.11
Zone 2		2.31	2.39	0.90	0.65	1.36	1.16	0.51	0.67	1.30	0.64	1.59	0.58	1.53	0.82	0.65	1.09
Zone 1		0.63	1.57	1.28	1.47	2.85	2.99	0.83	1.29	1.31	3.78	1.93	0.54	2.19	1.22	1.01	0.96
In tube		0.03	0.07	0.00	0.01	0.32	0.26	0.13	0.10	0.05	1.12	0.00	0.06	0.31	0.05	0.31	0.82
Standing		1.28	0.87	0.04	0.21	0.19	0.07	0.06	0.13	0.20	0.22	0.40	0.33	0.47	0.20	0.37	0.75
On roof		0.17	0.25	0.11	0.30	1.22	1.10	0.53	0.90	1.27	1.97	1.83	0.31	1.00	0.66	0.65	0.51
Grooming		0.12	0.17	0.65	0.16	0.45	0.40	0.11	0.39	0.20	0.17	0.30	0.26	0.25	0.31	0.16	-0.36
Eating		0.05	0.03	0.05	0.02	0.02	0.02	0.01	0.02	0.02	0.01	0.08	0.03	0.02	0.03	0.02	-0.51
Stretching		0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.01	0.03	0.06	0.01	0.02	0.02	-0.66
In nest box		0.05	0.13	0.14	0.30	0.20	0.53	0.32	0.90	0.15	0.31	0.48	0.24	0.23	0.40	0.23	-0.71
Total no. activities		4.01	4.46	2.33	2.42	5.53	6.18	1.88	3.57	3.03	5.52	4.42	1.20	4.79	2.64	1.58	1.36

Table 2. Pearson Correlations of frequency of different behaviours displayed by female *S. douglasi*. Significance value (2-tailed): * p<0.5, ** p<0.01, ***p<0.001.

Behaviour	**Zone 3**	**Exercise**	**Encounters**	**Zone 2**	**Zone 1**	**In tube**	**Standing**	**On roof**	**Grooming**	**Eating**	**Stretching**	**In nest box**
Zone 3	…											
Exercise	0.85***											
Encounters	0.69**	0.85***										
Zone 2	0.37	0.51	0.33									
Zone 1	084***	0.59*	0.58*	-0.07								
In tube	0.62*	0.19	0.21	-0.26	0.79***							
Standing	0.15	0.18	0.05	0.83***	-0.31	-0.19						
On roof	0.59*	0.24	0.06	-0.12	0.73**	0.61*	-0.31					
Grooming	-0.04	0.20	0.22	-0.17	0.19	-0.13	-0.47	-0.01				
Eating	-0.14	-0.03	-0.20	0.47	-0.25	-0.45	0.39	-0.01	0.24			
Stretching	-0.55	-0.72**	-0.56	-0.21	-0.39	-0.13	0.03	0.05	-0.26	0.22		
In nest box	0.11	0.15	0.08	-0.42	0.18	0.06	-0.44	0.36	0.21	-0.11	-0.11	…

2.3.4 Fail safe N

Fail safe N (see page 36 for more details) was calculated to indicate the number of studies that would be required to reduce the effect size observed in a particular study to a non-significant value (Rosenthal 1979, Hedges & Olkin 1985).

In the current study k_0 (zone 3)= 1(1.42-0.1)/0.1=13.2 and k_0 (in nest box)=1(-0.71-0.1)/0.1=-6.1. Therefore, in order for the effect size of the behaviour classified as "entering zone 3" and "in nest box" in this study to be reduced to a non-significant value (0.1; Cohen 1988), data from a further 39 animals (13 studies with three animals each) observed for entering zone 3 and 18 animals (six studies with three animals each) observed for entering the nest box would be required, all of which would have to generate effect sizes of less than 0.1.

2.3.5 Observation time and accuracy of the model

The predictive power for periods of observation of 1x5-minute, 2x5-minute and 3x5-minute were calculated and are depicted in figure 3. PPP increases from 72% to 82% with a change from one to two five-minute periods of observation while NPP increases from 86% to 95% with the same increase in number of observation periods. There is a small decrease in OPP, from 89% to 88%, with an increase from two to three five-minute observation periods. This is in accordance with a decrease in PPP from 82% to 75% within the same increase in observation time. NPP increases from 95% to 100% when adding a third 5-minute observation period. However, addition of a third observation period does not improve OPP.

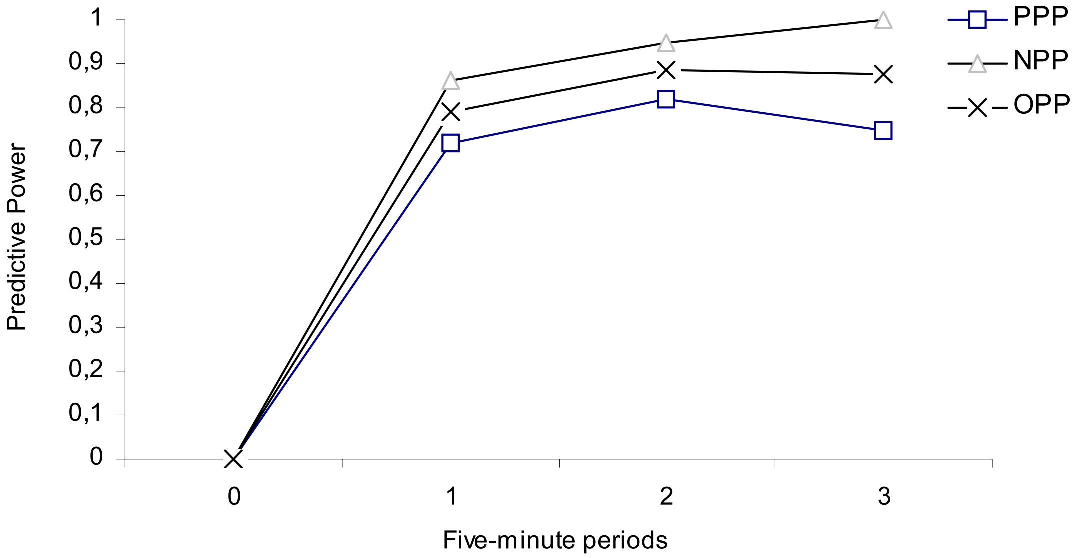


Figure 3. Predictive power of the discriminant function used for predicting the reproductive state of female S. douglasi, as a function of observation time counted in random five-minute blocks

Predictive powers of Figure 2 when testing 2x5-minute epochs are presented in Table 3. The PPP was 0.82 indicating that 82% of the cases in which the female was identified as being in oestrus, she was. Accordingly, a NPP of 0.95 indicates that on 95% of occasions, non-oestrus females were correctly identified as not being in oestrus. Consequently, on 18% of occasions, females that were in oestrus were incorrectly identified as non-oestrus and on 5% of occasions a non-oestrous female would be incorrectly identified as oestrous.

Table 3. Positive Predictive Power (PPP), Negative Predictive Power (NPP) and Over-all Predictive Power of Figure 2, based on 47 2x5-minute observation periods of female *S. douglasi*.

PPP	0.82
NPP	0.95
OPP	0.89

2.3.6 Cross-validation of the discriminant function

To evaluate the accuracy of the discriminant function, it was cross-validated with four new females. The results are presented in Table 4. For these four females the PPP decreased to 0.66 and represents a reduction in predictive accuracy from the value of 0.82 reported in the sample of animals used to develop the function (Table 3). Similarly, the NPP decreased to 93%, resulting in the overall predictive power being reduced to 79 % (Table 4). The implications of this are that while approximately the same number of females is likely to be falsely identified as not in oestrus, it appears that approximately one in three females (34%) would be falsely identified as in oestrus when they are not.

Table 4. Predictive Power of Figure 2 when verifying the equation with four new female *S. douglasi*.

PPP	0.66
NPP	0.93
OPP	0.79

One female, G6 frequently displayed stereotypic behaviour, i.e. “pacing” or “weaving” (Mason 1991; Wiedenmayer 1997), when she, for no apparent reason would run invariantly from one side of the cage to the other for long periods of time without stopping to engage in any other activities. Stereotypic behaviour is rarely observed in free-living animals and is assumed to be a response to impoverished physical and behavioural environmental conditions in captivity (Mason 1991; Kiley 1997). Stereotypic behaviour exhibited by female G6 may have been a consequence of this individual not using the exercise wheel for running (discussed below, chapter 4). Consequently, the count of "entering zone 3" was very high in those instances when this individual displayed pacing during the observation periods. This is likely to cause an artificially high Activity score and thereby generate an error when included in the calculations for PPP (the probability of the female truly being in oestrus when receiving an oestrous or positive Activity score). To assess this effect, the accuracy of the equation (Figure 2) was tested with the occurrences where female G6 displayed excessive pacing excluded. After exclusion, the total sample included 20 oestrus and 19 non-oestrus periods in total. This approach increased PPP dramatically from 66% to 86%, which resulted in an increase of OPP from 79% to 90% (Table 5). This suggests that females would be incorrectly identified as in oestrus on approximately one in seven occasions (14%).

Table 5. Predictive Power of Figure 2 when verifying the equation with four new female *S. douglasi,* excluding occurrences of pacing.

PPP	0.86
NPP	0.94
OPP	0.90

2.4 Discussion

2.4.1 Timing, body weight and food consumption during oestrus

The timing of onset of oestrus did not appear to be synchronised among the females, as both cycle length and oestrus duration varied between the different individuals. However, this does not contradict the onset of oestrus by environmental cues reported previously (Godfrey 1969b; Selwood 1985; Scott 1986; McAllan & Dickman 1986; Joss & Firth 1991), as these studies referred to the onset of the reproductive season rather than time between individual oestrus cycles. The oestrus cycle length in *S. Douglasi* (10-21 days, mean 18.1 days) was shorter than that reported for other Sminthopsis species; a mean of 31.1 days in *S. crassicaudata* (Smith, Bennett & Chesson 1978), 23.3 days in *S. macroura* (Woolley 1990), 26.2 days in *S. larapinta*

(Godfrey 1969a), 23.8 days in *S. murina* (Fox & Whitford 1982) and 32.6 days in *S. virginae* (Taplin 1980). Oestrus length (cornified cells present in the urine) in *S. Douglasi* (4-7 days, mean five days) was similar to 2-9 days, mean 5.2 days in *S. larapinta* (Godfrey 1969a), and 3-9 days, mean 6.3 days in *S. macroura* (Woolley 1990).

This study showed were no significant changes in weight and food consumption coinciding with oestrus, such as those reported by Woolley (1984; 1990). However, this may be partially due to the large numbers of zero values for the leftover-food parameter in this data set, which may compromise the power of the statistical test used (Zar 1999).

2.4.2 Targeting initial behaviours

Measurements used to study behaviour should reflect the nature of the problem and the questions asked (Martin & Bateson 1993). A 'fine-grained' analysis is only appropriate for answering some sorts of questions, and a full understanding will not necessarily emerge from describing and analysing behaviour at the most detailed level. The cost of gaining detail can be that higher-level patterns, which may be the most important or relevant features, are obscured (Martin & Bateson 1993). The purpose of this study was to find a way of determining reproductive state in female *S. douglasi* by observing the behaviour of the animals for a relatively short period time. Infrequent or cryptic behaviours were therefore inappropriate as a focus in the present study.

While it may seem unusual that no other behaviours were retained in the discriminant function, it is the case that inclusion of any of the remaining ten variables failed to increase the predictive accuracy.

2.4.3 Statistical Design

A frequently encountered problem when studying a rare or endangered species is obtaining a sufficiently large number of subjects. Thus the methods that need to be employed in studying rare species must acknowledge and permit robust measurement in a restricted sample size. This may be achieved by utilising a large number of behavioural observations on a small number of animals. This strategy maximizes the amount of useful data obtained from the small sample size of the animals available and uses this data in the most appropriate way to support the study objectives.

It can be difficult to infer characteristics of a group from the behaviour of an individual, and vice versa, as statements about the characteristics of a group may be untrue for some individuals in the group (Martin & Bateson, 1993). The statistical techniques that are usually used for analysing behavioural data are designed primarily for drawing inferences from groups, rather than from individuals. A common aim is therefore to avoid the confounding effects of individual differences in behaviour and to emphasise what members of a population have in common. However, some of the behavioural differences between individuals are of considerable biological significance and should not be dismissed as mere statistical noise (Martin & Bateson 1993). Behavioural biologists have abandoned the notion that characteristics may necessarily be generalised to all members of the species (Martin & Bateson, 1993; Krebs & Davies 1997). For example, Bateson and Young (1981) constructed a growth curve for a group of domestic kittens (*Felis catus*). The average growth curve was found to be unrepresentative of any individual kitten in the group. Their model fitted the group as a whole, but it could not validly describe the growth pattern for any of the kittens.

The objective of the present study was to examine the behaviour of individual animals. This study does not take account of group dynamics. The experimental design and statistical methods utilised reflect these intentions and employ approaches consistent with single-case experimental design. Thus, each animal is regarded as an experiment and each subsequent animal, a replication. Repeated measurements improve statistical power by reducing the effects of random measurement error (Martin & Bateson 1993). Each individual is observed repeatedly before, during, and after the experimental condition (oestrus) has occurred. Thus, baseline measurements are obtained allowing each individual's response to be expressed as the difference between its non-oestrus baseline and oestrus state, i.e. the change in its behaviour.

2.4.4 Fail safe N

The high value of the Fail-safe N calculations (data from another 13 identical studies, all with non-significant results, is required in order to reduce the result to a non-significant value; Cohen 1988) strongly suggests that although only a small number of animals (n=3) were employed in the current study, the likelihood that significant effects would not have been found with a larger sample size is extremely low.

2.4.5 Observation time and accuracy of the model

After the initial two random five-minute periods of observations, little was gained in accuracy of the model by adding further observation periods (Figure 1). This implies that two 5-minute periods of observation is the most appropriate option when applying the suggested model to *S. douglasi* under the present operating conditions.

The overall accuracy of the model (89%, Table 3) is a remarkably good result considering the small number of females in the study (n=3) and the relatively brief periods of observation (2x5 minutes) under consideration. The lower PPP compared to NPP is "undesirable" in that if a female is falsely classified as oestrous and paired with a male, there is a substantial risk of injury to one or both animals, an unwanted outcome. Conversely, if a female is falsely classified as non-oestrous it will only result in a missed mating opportunity, which, while unfortunate, poses no potential threat to either male or female.

2.4.6 Cross-Validation of the Discriminant Function

Positive predictive power increased to 0.86 when cross-validating the model with new females, indicating that females would be incorrectly identified in 14% of the cases. Although this is a remarkably low number, this is an undesirable outcome, as placing a non-oestrus female *S. douglasi* in a confined space with a male *S. douglasi* poses some threat to the well-being of one or both animals. The traditional method of urine sample analysis is believed to have a higher accuracy (Godfrey 1969a). On the other hand, this requires daily handling and sampling, which is intrusive and distressing to female *S. douglasi*. However, an appropriate combination of methods may produce optimal results. Daily observations of two random five-minute periods, examining the number of times the female enters zone 3 or the nest box would be expected to produce estimates of oestrus with almost 90% accuracy. Urine could subsequently be examined for the presence of cornified cells at that time to confirm oestrus state. This combination of methods would dramatically reduce handling of *S. douglasi* and also reduce the number of urine samples requiring examination. Urine sampling and subsequent examination for cornified cells would become a confirmatory procedure. This approach would avoid the likelihood of injury to one or both animals on approximately one in seven occasions when behavioural observations yield a false positive prediction of oestrus.

In conclusion, observing behaviour of female *S. douglasi* during two random five-minute periods where the number of times that the female enters the zone farthest away from the male and number of times she enters the nest box are recorded can enable the reproductive state to be identified with an accuracy (OPP) of 90%. The accuracy of this method was confirmed by testing the proposed method on four new female *S. douglasi* with a similar outcome. However, care should be taken to not to use observation periods when the animal is displaying stereotypic behaviour such as pacing, as this will produce confounding results. Application of this method may considerably reduce the amount of handling required in the husbandry of this animal.

Chapter 3

Study 2 - Observing behaviour in different social contexts

3.1 Introduction

The results of study 1 identified those behaviours that were most predictive of oestrus and generated a discriminant function that identifies oestrous state in *S. douglasi* with an overall accuracy of 90% (Tables 3 and 5). Additionally, the optimal observation time was identified as two random five-minute periods of observation. However, all observations have been made in a context where the observed female has been situated in close proximity to a male *S. douglasi* (Figure 1). The assumption is that the presence of a male will trigger a response that influences the behaviour of the female. Although the discriminant function requires observation of only the female, the presence of the male may be sufficient and necessary to evoke the targeted behaviours. If this is the case, then the use of the discriminant function and such brief periods of observation would only be valid in those breeding colonies where the housing arrangements are identical to those employed in study 1. Accordingly, the aim of study 2 is to examine the impact of different housing arrangements on the predictive accuracy of the discriminant function. To accomplish this, the male was removed and replaced with another female *S. douglasi* or alternatively not replaced at all and the studied female was caged alone.

3.2 Method

3.2.1 Observations

Four female *S. douglasi* were observed using observation methods identical to those described in sections 2.2.2-2.2.4; 2.2.9. The animals were examined daily for general health and urine samples. Observations were carried out by video recording during a six-month period; June – November 2004. During this period they were housed on the right side on the monitor enclosure (Figure 1) in three different social contexts; adjacent to a male, adjacent to a female or singularly in a Latin Square Design (Cochran & Cox 1992). A total of nine oestrous and 16 non-oestrous observation periods were obtained from a female accompanied by another female. Twelve oestrous and 18 non-oestrous observation periods were obtained from single females and 20 oestrous and 19 non-oestrous periods were observed in female-male context (same data used in 2.2.9). This excluded the observation periods of female G6 when she was engaging in excessive stereotypic behaviour (see section 2.3.4).

3.2.2 Statistical design

The mean AS of oestrus females compared to non-oestrus females in each of the three social contexts were analysed statistically using a Kruskal-Wallis non-parametric test (Zar 1999). Also, mean AS of only the observations of oestrous females were analysed, comparing the differences in AS between females in the three different social contexts using a Kruskal-Wallis test. The same was done analysing only the observations from non-oestrus females.

Occurrences of entering zone 3 and the nest box were recorded (behaviours described in section 2.3.8) and entered into the following function according to study one:

Activity score (AS) = 1.708 x zone 3 – 4.434 x on nest box – 2.089
If AS is positive (AS>0) then predict oestrus, If AS is negative or equal to zero ($AS \leq 0$) then predict anoestrus.

The Activity score (AS) was compared to the physiological signs of oestrus (presence of cornified cells in the urine) and predictive power was calculated as described in section 2.2.7.

3.3 Results

Data from social context and reproductive state is presented in Appendix 2. Oestrous females had a statistically significant higher activity score than non-oestrous females regardless of whether they were accompanied by a male (Kruskal-Wallis test, χ^2=24.42, df=1, p<0.001, Figure 4), accompanied by female (Kruskal-Wallis test, χ^2=7.09, df=1, p=0.008, Figure 4) or if they were alone (Kruskal-Wallis test, χ^2=8.18, df=1, p=0.004, Figure 4). However, there was no significant difference in activity score between oestrous females in these three social contexts (Kruskal-Wallis test, χ^2=2.85, df=2, p=0.241, Figure 4) or between non-oestrous females in these different social contexts (Kruskal-Wallis test, χ^2=2.04, df=2, p=0.361, Figure 4). Thus, activity score is higher during oestrous than in non-oestrous in females, whether accompanied by a male, female or alone. There is no significant difference between oestrous females accompanied by a male female or single, or between non-oestrous females in these three social contexts.

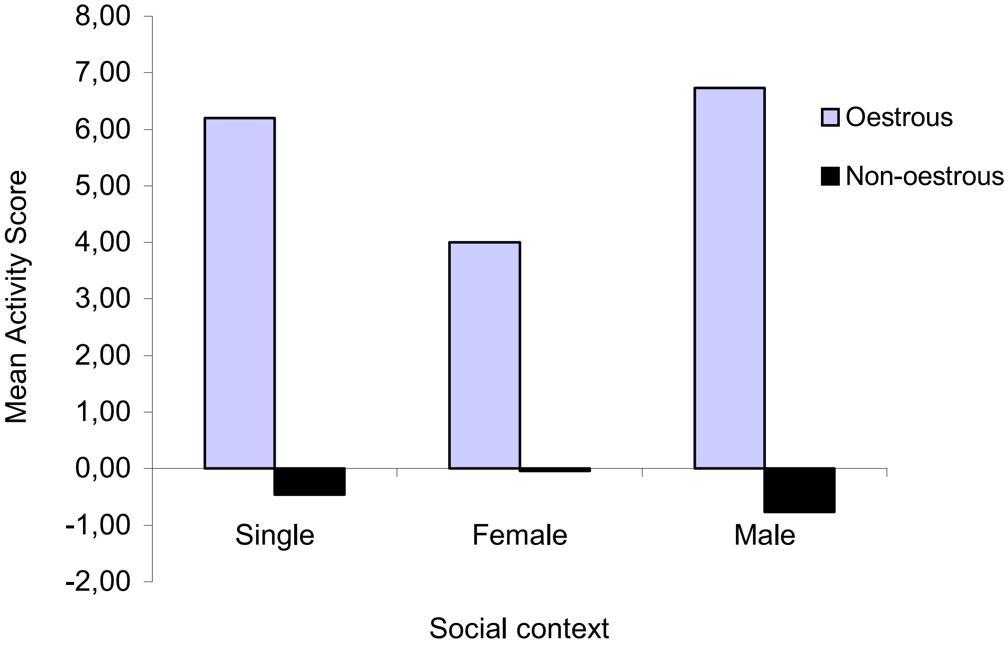


Figure 4. Mean value of Figure 2, AS (Activity score) = 1.708 x Zone 3 – 4.434 x in nest box – 2.089 , in oestrous and non-oestrous female *S. douglasi* accompanied by a male, a female or single. Oestrous females had a statistically significant higher activity score than non-oestrous females regardless of whether they were accompanied by a male (Kruskal-Wallis test, χ^2=24.42, df=1, p<0.001, Figure 3) if they were accompanied by female (Kruskal-Wallis test, χ^2=7.09, df=1, p=0.008) or if they were in a single context (Kruskal-Wallis test, χ^2=8.18, df=1, p=0.004). However, there was no significant difference in activity score between oestrous females in these three social contexts (Kruskal-Wallis test, χ^2=2.85, df=2, p=0.241) or between non-oestrous females in these different social contexts (Kruskal-Wallis test, χ^2=2.04, df=2, p=0.361)

The predictive power obtained when testing the accuracy (see 2.3.3) of Figure 2 is presented in Table 6 (female company) and Table 7 (single). The PPP is greatly reduced under both contexts (Tables 6 and 7) in comparison to the female-male context (Tables 3-5), from 86% female-male to 50% female-female and 57% single. The NPP is still relatively high (82% female-female and 75% single), and results in an OPP of 66% under both conditions (Tables 6 and 7). This suggests that even though the pattern of increased activity during oestrous is evident in females in all three contexts (single, male company and female company); accuracy of the model developed in the previous chapters is not maintained in different social contexts. The lower values of PPP suggest that overall activity of the female has been reduced in these different social contexts.

Table 6. Predictive Power of Figure 2 when verifying the equation with female-female couples of *S. douglasi*.

PPP	0.50
NPP	0.82
OPP	0.66

Table 7. Predictive Power of Figure 2 when verifying the equation with single females of *S. douglasi*

PPP	0.57
NPP	0.75
OPP	0.66

3.4 Discussion

In conclusion, the trend of increased activity during oestrus is significant in female *S. douglasi* regardless of the housing context. However, use of the model presented in Study 1 (Figure 1) in contexts where the female is in close proximity to another female or single is not as accurate as when the female is housed next to a male. This is probably because overall activity of the female is reduced somewhat in the different social contexts. Another function may be generated by discriminant function analysis, where the behaviors are weighted (preceded by different coefficients in the equation) to suit the different activity mode, in order to identify the reproductive state in females in different social contexts more accurately.

Chapter 4

Automatic measurement of activity

4.1 Introduction

One of the intriguing results from study one was that despite a wide range of behaviours under observation, only two (entering zone 3 and the nest box) contributed to the accurate prediction of oestrus state. A likely explanation for this is that the most apparent aspect of the animal's behaviour is general level of activity. As the activity level increases during oestrus, several of the originally observed behaviours increase in frequency as well. Zone 3 was the behaviour that best represented the increased activity level and was therefore used in the equation (figure 2). If this is the case, then potentially the observation of activity level could be an automated procedure that requires no direct observation of animals or the use of videotapes. The advantages of using an automatic device to measure activity, instead of analysing the two discrete five-minute observation periods indicated in study 1, are the reduction in time required by the observer and the potential for continuous recording over the entire active period.

Oestrus behaviour has been examined in sows by Altman (1941) and in dairy cows by Farris (1944), using mechanically activated pedometers attached to the legs of the animals to count steps as a measure of physical activity. Kiddy (1977) further developed pedomery as a practical tool for detection of oestrus in cattle. He found that cows in oestrus were 3-4 times more active than cows not in oestrus. Since then, pedometry has been widely applied as a tool in cattle industry (Koelsh, Aneshansley & Butler1994; Senger 1994; Wangler et.al. 2005).

The aim of this part of the study is to investigate whether it is possible to measure activity and identify reproductive state of the female *S. douglasi* through an automated procedure that requires no direct observation of animals or videotapes. One such method is to measure how far the female ran in her exercise wheel. Exercise wheel running has been used as a measurement of activity in previous studies of small mammals e.g. the prairie deer mouse (*Peromyscus Maniculatus bardi*; Cushing 1985), the golden hamster (*Mesocricetus auratus*; Carmichael, Nelson & Zucker 1981) and the eastern quoll (*Dasyurus viverrinus*; Kennedy, Coleman & Armstrong 1990).

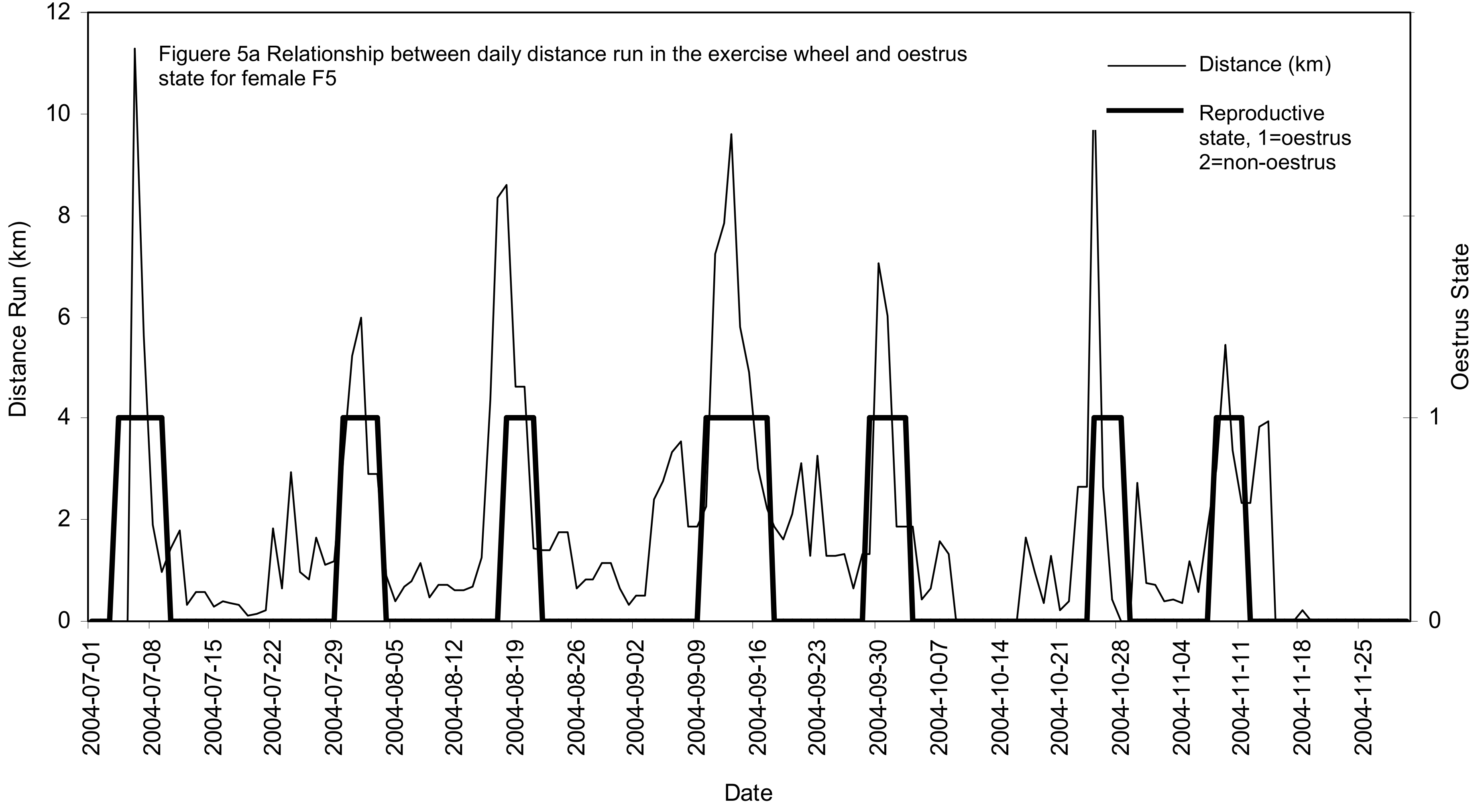
4.2 Methods

A bicycle computer (Techwell, Mate 3) was attached to the exercise wheel in the cage (Figure 1) of four of the females in the second part of the study described in section 2.2.9 and chapter 3. Most of the females in the study made extensive use of their exercise wheel. One female (G6), however, stopped using the exercise wheel for no apparent reason after the commencement of the study (see section 2.3.4). Thus, Female G6 was not included in the analysis of the exercise data. In total, 380 days (24-hour periods) of activity; 87 oestrus (26 days of female F5, 26 days of female F19 and 35 days of female G7) and 293 non-oestrus (91 days of female F5, 92 days of female F19,110 days of female G7) were recorded during a five-month period; July – November 2004. The bicycle computer measured and recorded distance, time, maximum speed and average speed with which the female had been running in the exercise wheel. Observations of the video recordings confirmed that each exercise wheel was only in motion when a dunnart was using it, and that it did not continue spinning after the dunnart had left the exercise wheel. The trip data was recorded and the bicycle computers were reset daily at approximately 3 pm (EST).

Distance run over a 24-hour period in the exercise wheel was compared during oestrous state compared to non-oestrous state for each of the three females with two-tailed, two-sample t-test using SPSS 12.0 (Zar 1999). The daily distance run in the exercise wheel by females in oestrus compared to non-oestrus was also analysed using discriminant function analysis (Hotelling 1935; Huberty 1994, see section 2.2.6) using SPSS 12.0.

4.3 Results

Data of wheel running activity is presented in Appendix 2. There was a highly significant increase in the distance run in the exercise wheel by all three females in the study when they were in oestrus compared to non-oestrus (female F5: t-test, $p<0.001$, df=113; female F19 t-test, $p<0.001$, df=113; female G7, t-test, $p<0.001$, df=137). Distance run by female *S. douglasi* and their reproductive state (oestrus/non-oestrus) are graphed against time in Figure 5a-c. However, discriminant function analysis of distance run over time produced a goodness-of-fit statistic, R^2_c (see 2.3.1) of 0.198, which is considerably less than that of the behavioural observation function derived in study 1 (0.759).



Figuere 5a Relationship between daily distance run in the exercise wheel and oestrus state for female F5

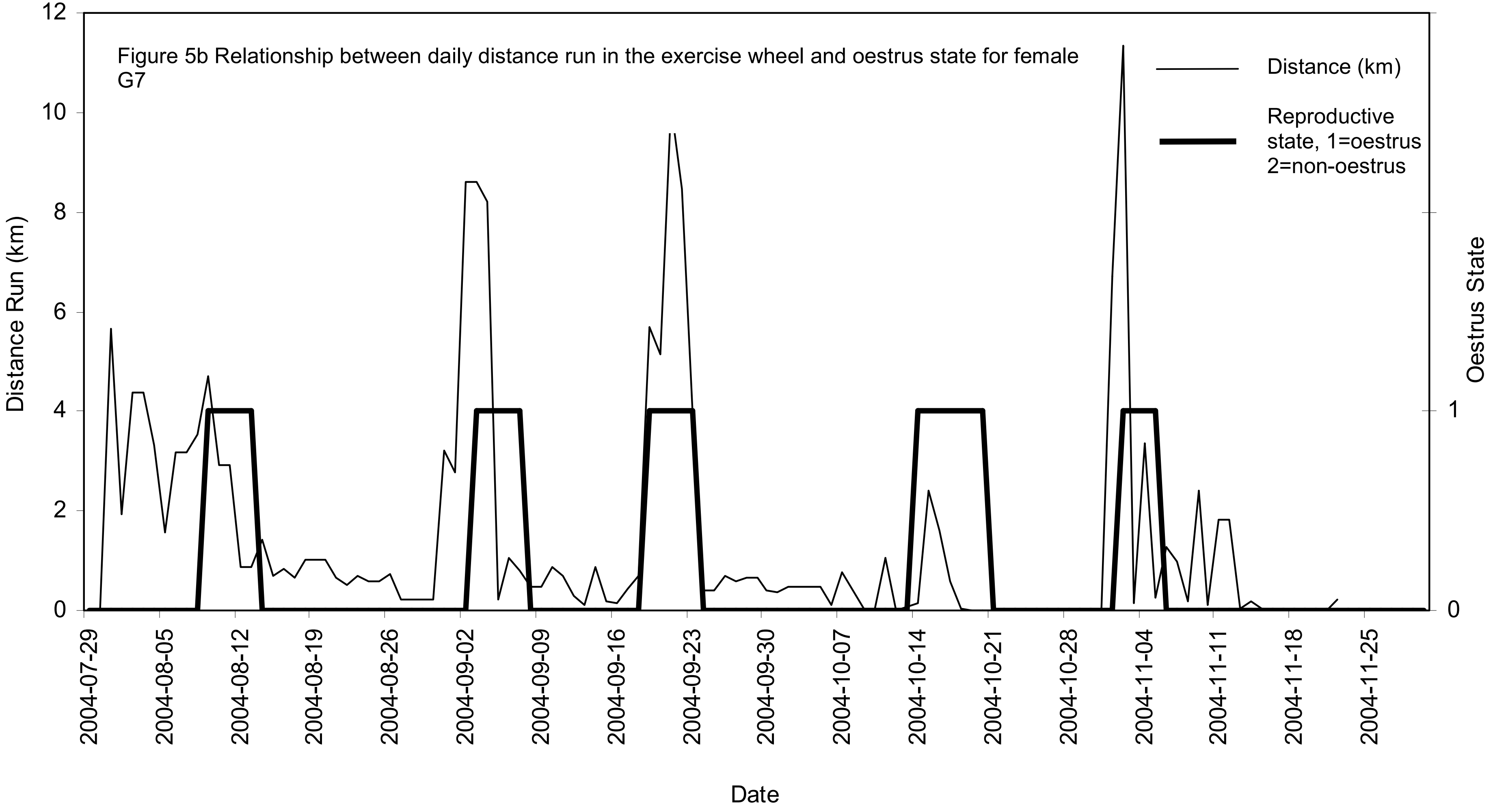


Figure 5b Relationship between daily distance run in the exercise wheel and oestrus state for female G7

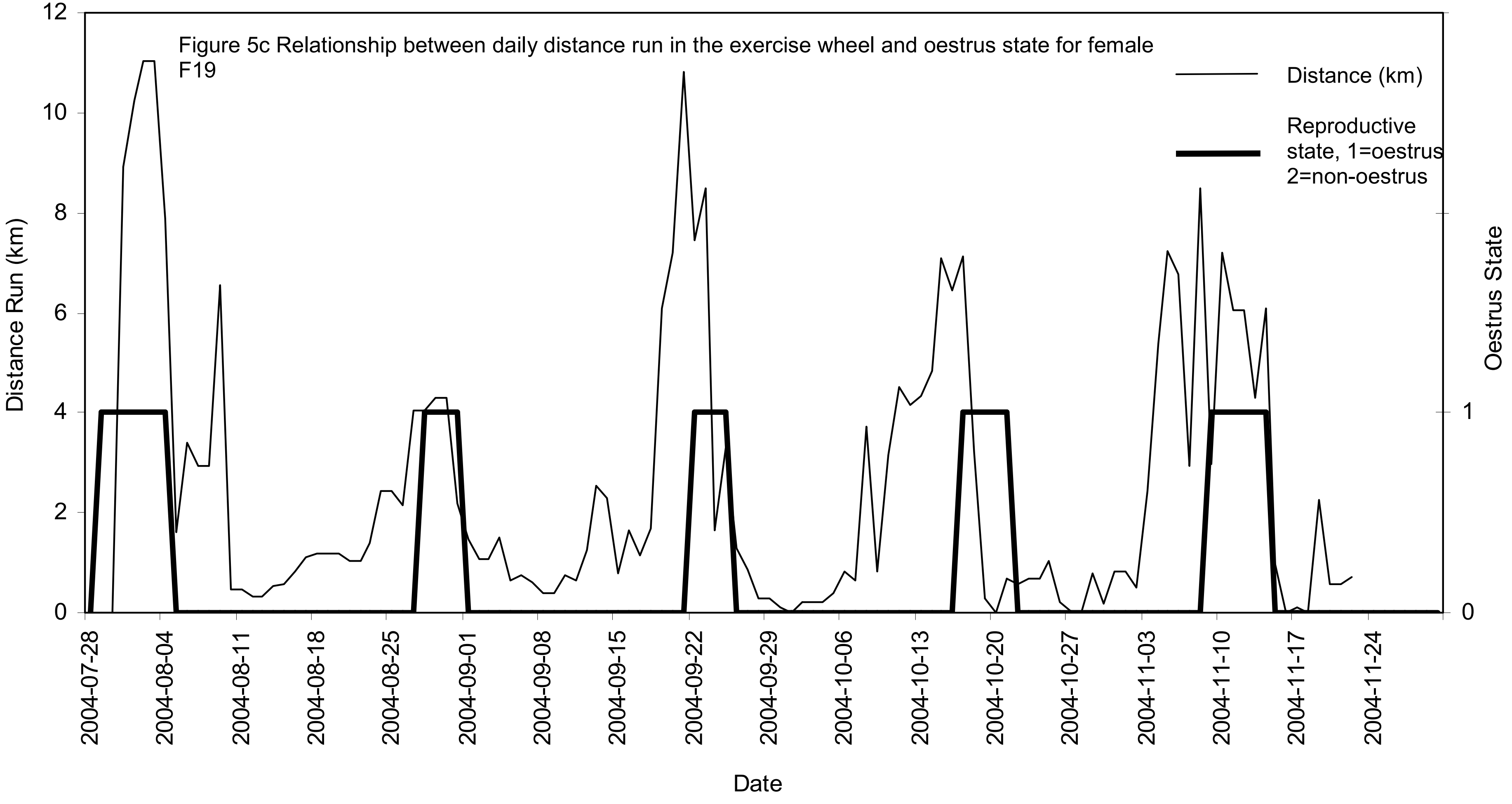


Figure 5c Relationship between daily distance run in the exercise wheel and oestrus state for female F19

Figure 5 a-c. The distance (kilometres) run in the exercise wheel (thin line) and the reproductive state identified by presence / absence of cornified cells in the urine of female (thick line) *S. douglasi*. Oestrus State: 1=oestrous, 0=non-oestrous.

4.4 Discussion

A very striking increase in distance run coincides with oestrous (Figure 5a-c). This confirms the previous findings of this study based on video-recordings of behaviour that activity levels of *S. douglasi* increase during oestrus. Furthermore, these results (Figure 4a-c) suggest that exercise wheels and trip computers may be successfully utilised to identify the reproductive state of a female *S. douglasi* without physically disturbing the animal. The automated recording system based on an exercise wheel with an attached bicycle computer has a lower R^2_c compared to the two five-minute observation periods proposed in study 1. This means that a lesser amount of the variation in the dependent variable (reproductive state) is explained by the independent variables (distance run in the exercise wheel). The automated procedure, may for that reason, not be preferred over the direct 2x5 minute observations. However, an exercise wheel with a bicycle computer attached is an inexpensive set-up that takes seconds to read and can, therefore, be very useful in animal husbandry situations involving breeding of small mammals and where resources are limited. As discussed in study 2, a combination of methods could be used. Urine could be examined for the presence of cornified cells to confirm a positive oestrus result predicted by the computerised method. This combination of methods would dramatically reduce handling of *S. douglasi* and also reduce the number of urine samples requiring examination. Urine sampling and subsequent examination for cornified cells would become a confirmatory procedure.

On several occasions, individual *S. douglasi* ran distances of over eleven kilometres in the exercise wheel during a 24-hour period. This does not include the distance the dunnart moved throughout the rest of the enclosure. Eleven kilometres is a much longer distance than might be expected from reports of mobility of this and similar species in literature. Eleven kilometres is a remarkable distance for an animal of such small size (40-70g) to run in a 24-hour period. There are reports in the literature of long-range movements of *Sminthopsis spp*. for example, up to twelve kilometers in *S. youngsoni* (Dickman 1996). However, this distance was measured over a time period of 18 months. (Dickman 1996) suggested that this movement in *S. youngsoni* was a response to local rainfall patterns and that the animals moved in order to locate food resources, i.e. these movements were not associated with reproduction. In contrast, the present study found that movement increased significantly when female *S. douglasi* were in oestrus. However, this result was obtained from dunnarts in captivity and it may not be valid to extrapolate these results to free-ranging animals in the wild. One obvious difference between the captive and free-ranging situations is that the captive dunnart is running this distance, but has not actually travelled to a different geographical location.

The trip computer used in the present study did not indicate the distribution of running activity in the exercise wheel during a 24 hour period. A set-up that enabled collection of such data could provide useful information on daily activity rhythms of *S. douglasi*.

In conclusion, the distance that a female *S. douglasi* ran in the exercise wheel coincides closely with her reproductive state; longer distances are covered while in oestrus. Reproductive state of female *S. douglasi* could be identified by attaching a trip computer to an exercise wheel and obtaining a continuous reading of distance run without any human interaction with the animal. Combining a positive oestrous result gained by this method with urine sample analysis could provide a very reliable way to identify the reproductive state of female *S. douglasi* and that of other small mammal species, with minimal handling of animals. *S. douglasi* is capable of running over eleven kilometres per night over several consecutive nights, which may have implications for the spatial distribution of the species in the wild.

Chapter 5

General discussion

5.1 Conclusions

5.1.1 Summary

The aims of this study were to develop a method to identify specific behaviours of *S. douglasi* that could be used to detect oestrus, and describe how this method could be incorporated into management of the species. This provides an easy, non-invasive complement to urine sample analysis in order to know when the female was in oestrus and ready to be paired with a male. These aims have been achieved. A method is presented where two random five-minute periods of observation of the behaviour of female *S. douglasi* can be used to identify reproductive state with 89% over-all accuracy. This is a satisfactory result, considering the relatively short observation period of 2x5 minutes which generated this accuracy. A large range of behaviours was initially investigated as potential predictors of reproductive state, however, the data indicates that only two behaviours are suitable. These were the frequency with which the female enters the area of the enclosure furthest away from the male (which also contained an exercise wheel), and the frequency with which the female retires into the nest box. During oestrus, the general level of activity increases above that during non-oestrus, so several behaviours are multicollinear. The fact that the frequency of entering the area furthest away from the male was the best predictor of oestrous state, does not indicate that the female is avoiding the male during oestrus. The frequency of entering the area of the enclosure closest to the male and the frequency of female-male encounters also increased during oestrus. However, since the increases of these behaviours are intercorrelated, only the best predictor remained in the DFA. It is possible that the presence of an exercise wheel in the zone further away from the male was the reason for the female's frequent visits to this area.

After the method was developed, it was tested on a new independent sample of females and the accuracy of the results (an over-all predictive power of 90%) was confirmed. When the context was changed from the female being in close proximity to the male to the female being accompanied by another female or being single, the same activity pattern was identified. The activity levels of female *S. douglasi* were significantly higher in oestrus compared to non-oestrus regardless of the social context. However, the method developed to identify oestrus in the context of a female accompanied by a male could not be applied as accurately in different social contexts.

5.1.2 Why does activity increase during oestrus?

The word oestrus comes from the Greek "oistos" which means "frenzy" (Hutchinson Encyclopaedia 2000). This translation seems particularly suitable in the case of *S. douglasi*. Why is it that the activity of female *S. douglasi* increases so dramatically during oestrus? There are no reports in the literature of this particular phenomenon in *Sminthopsis spp.* or other dasyurid species. However, there are several studies suggesting that activity increases significantly during oestrous in other mammals, such as white rats *Rattus norvegicus* (Wang 1923; Slonaker 1924; Farris 1944; Finger 1969; Steiner, Kratz & Carroll 1982; Wollnik & Turek 1988), sows *Sus scrofa domesticus* (Altman 1941), dairy cows (Farris 1954; Kiddy 1977; Senger 1994), prairie deer mice *Peromyscus maniculatus bairdi* (Cushing 1985) and golden hamsters *M. auratus* (Lisk, Ciaccio & Catazarol 1983). Cushing (1985) suggested that the behaviour patterns of oestrus *P. Maniculatus bardi* is a way to increase scent marking of the surroundings in order to advertise their reproductive state and attract a mate. Such advertisement may also occur in *M. auratus* (Lisk, Ciaccio & Catazaro 1983) and meadow voles, *Microtus pennsylvanicus* (Madison 1980 a;b). Increased activity, which in turn leads to increased scent marking, would attract males and thus encourage them to move into or visit a female home range to a greater extent in species that generally do not have overlapping home ranges (Madison 1980a;b; Lisk, Ciaccio & Catazaro1983; Cushing 1985). Mifsud (1999; 2001) suggest that *S. douglasi* occupies a stable home range that overlap those of several other males and females of the same species. If this is the case, it may be possible that increased activity of oestrous females facilitates an increase in scent marking and thereby attracts more males to the home ranges of the oestrous females. However, several studies of other *Sminthopsis spp*. (Morton 1978b; Dickman, Predavec & Downey 1995) as well as *Planigale spp*. Read (1984b; 1989) state that the home ranges of these species are "drifting home ranges" where both females and males continually shift home ranges and do not appear to defend a territory at any time (with the exception of breeding females). If that is the case in *S. douglasi*, the increased scent marking theory put forward in Madison (1980a;b), Lisk, Ciaccio & Catazaro (1983) and Cushing (1985) is not applicable. However, increased activity during oestrus may also be a direct way to actively search for a mate. Even without a change in the number of males in the female's surroundings, a female who increases her activity, rather than just waiting for the male to detect her would increase her chances of encountering a male (Cushing 1985).

It is possible that a species such as *S. douglasi*, that normally lives under conditions where its population density is very low (pers. obs.) has a higher activity level during oestrus in order to increase the probability of finding a suitable partner during the relatively short timeframe of oestrus (3-5 days, pers. Obs). However, it is important to note that all the findings of the present study were obtained from a captive population. A study of populations in the wild may produce different results. Thus, a comprehensive field study would be needed to confirm this result in free-ranging *S. douglasi*.

5.2 Critique of the study

5.2.1 Time of observation

One aspect of this study is that all observations were made during the period of the day when *S. douglasi* are most active i.e. during the night (Crowcroft & Godfrey 1968; Ewer 1968; Hall 1980) from approximately 3.30 pm to 6.00 am (EST). The results of the present study may not be valid when generalised to the behaviour of *S. douglasi* during other periods during the day. However, this may not constitute a major problem in this case, as the *S. douglasi* were inactive for most of the time during the day (personal observation). Perhaps, the greatest limitation is that the species under consideration in the present context is nocturnal while those who wish to observe its behaviour in order to predict oestrus state are generally not. Nonetheless, two five-minute periods of observations in which the frequency of two well-defined behaviours must be noted does not seem arduous and is a small price to pay in terms of time and effort in order to reduce the handling and physiological sampling of the female dunnarts.

5.2.2 Problems of a small sample size

A more appropriate experimental design to identify reproductive behaviour than that used in this research would be a balanced study, with an equal number of oestrous and non-oestrous epochs, of every social context from each female (Cochran & Cox 1992). This proved impractical with *S. douglasi*. The short time span of the female oestrous (3-5 days, Beckman 1997) was a limiting factor in the data collection. In addition, with very limited availability of animals to include in the study, there was no scope for “backup”.

The limitations imposed by reliance on a small number of animals can create difficulties when analysing data sets. Problems include violations of assumptions regarding the use of parametric statistical tests such as the analysis of variance (Zar 1999). The low sample size (n=4), uneven distribution across the data set and missing data points (due to equipment failure) made it impossible to analyse the data with a repeated measurement ANOVA or a paired sample t-test, which would otherwise have been appropriate. Instead Kruskal-Wallice tests were used. This is a non-parametric test that may have slightly less power than the parametric equality, but it relaxes the requirements for large sample size and normally distributed data and it is therefore more appropriate to apply on this data set (Zar, 1999).

Experimental designs and statistical methods employed in the biological sciences are usually associated with larger sample sizes that lend themselves to more group-based statistical analyses (Martin & Bateson 1993). However, when dealing with endangered species, small numbers of animals are ‘the rule, rather than the exception’. Methods must be employed which yield robust results, even with small sample sizes or single cases. For example, if a Tasmanian tiger (*Thylacinus cynocephalus*) was re-discovered, should scientists refrain from studying it because it is only one animal? In the present, study a method was developed, verified and tested under different contexts, which provided a way of identifying oestrus state in *S. douglasi* through behavioural observation with a high degree of accuracy. In addition, the large effect sizes (section 2.3.1) and the notable outcome of the Fail-safe N (section 2.3.2) indicate that the findings of the study are robust.

5.2.3 Improvements to the study

The enclosure set-up and the behaviours that were selected for observation appear appropriate and enabled the objectives of the study to be achieved. However, there are ways in which this study may be improved or extended. For example, vocalisations were not included in this research. Studies of similar species (Croft 1982; Fox & Whitford 1982; Read 1984a; Taplin 1980; Van-Dyck 1979) have suggested that the female utters "mate-attracting" calls when non-oestrous, a character that may be worth investigating in *S. douglasi*. Collecting data of vocalizations would require either an observer present in the room during the active period of the animals or a very sensitive recording device that could replay any sounds that were uttered, as well as identify the individual animal that emitted the call. This may present some problems, as it can be difficult to identify which animal made a particular sound when observing in a dark room with several animals present (pers. obs.).

In this study only the behaviour of the female was observed. An interesting extension to the study would be to investigate how the behaviour of the male *S. douglasi* is affected by the reproductive state of the female. Several studies (Ewer 1968; Maynes 1973; Braithwaite 1974; Ganslossner & Meisner 1984; Stead-Richardson et al. 2001; Van-Dyck 1979) have indicated that the behaviour of the male *S. crassicaudata, Macropus parma, A. stuartii, D. byrnei, D. geoffroii* and *P. maculata* changes when oestrous females of the same species are present. Examples of such changes include increased aggressive behaviour and increased incidence of behaviours such as cloacal marking and sniffing, which provide olfactory cues.

5.3 Future directions

5.3.1 Application of the model to other species

This study presents a novel approach to the study of reproduction and behaviour in dasyurids. To my knowledge only one other study has attempted to examine oestrus behaviour in dasyurids. Ganslosser & Meissner (1984) examined behaviour of quolls (*D. byrnei*) and noted that females do not tolerate the male (although they will tolerate other females) except when they are in oestrus. The present study examined the behaviour of female *S. douglasi* under specific conditions, and the discriminant function that was derived from this study should, therefore, only be applied to this species under the same conditions. However, the methodology developed in this study may be successfully applied to other dasyurid species, as well as to other groups of mammals. The methodology may be particularly useful in the housing and breeding of species that are rare or endangered, in particular, those that respond badly to handling. Unfortunately, the status of many Australian native marsupials is critical. Fifteen species (24%) of smaller dasyurids are classified as vulnerable, endangered, critically endangered or data deficient according to IUCN Red List criteria (Maxwell et al. 1996). Captive breeding and reintroduction programs have so far been limited. Examples of dasyurid species that has been bred systematically for reintroductions are the southern dibbler (*Parantecinus apicalis*; Friend 2004), the chuditch (*Dasyurus geoffroi*; Orell & Morris 1994) and the numbat (*Myrmecobius fasciatus*; Friend & Thomas 1995). Captive breeding is an important part of conservation of endangered species and needs to be integrated into recovery plans (Bradley et al. 1999; Wilson, Dickman & Fletcher 2003). The potential to breed animals with minimal contact with humans facilitates the creation of a breeding situation that would be expected to be more natural to the animal and characterised by reduce stress, which in turn avoids domestication. This is desirable in several situations for example captive breeding and releasing programs (Bradley et al. 1999).

5.3.2 Conservation status of *S. douglasi*

Most records of *S. douglasi* are scattered in time and consist of a small number of animals. Archer (1979) described the species based on four specimens; Woolley (1992) published new records of the species based on twelve individuals and Kutt (2003) found 14 individuals by trapping and predator gut collection. Mifsud (1999) reports higher numbers (127 individuals, excluding recaptures, caught over 28130 trap nights during 13 months in year 1996-1998) in Coolibah paddock at Proa, Queensland. Eighteen individuals (excluding recaptures) were caught over 2400 trap nights in July-August 2001 in Bladensburg National Park, Winton, Queensland (Mifsud 2001). However, recent trapping at the same area in 2003-2004 (this study, Appendix 1) showed a very low abundance. Only two individual *S. douglasi* were caught over 2694 trap nights. The reason for these large fluctuations in population size is unknown. It is possible that the severe climate changes that characterize this type of environment (Orr & Holmes 1984) cause variation in the density of *S. douglasi*, as resources are unpredictable (Morton 1978a;b).

The present study has showed that *S. douglasi* are capable of traveling long distances in a relatively short period of time (up to eleven kilometers per night). Accordingly, it is possible that numbers of *S. douglasi* do not decline when resources are scarce, but that many *S. douglasi* simply relocate to different areas where resources are more abundant. In either case, *S. douglasi* is an endangered native marsupial that only lives in a specific habitat and is restricted to a small geographical area. Continued active work for conservation of this and similar species is necessary in order to secure the future of the species. Breeding populations in captivity is an important part in conservation practices. This study can enhance the success of breeding the species in captivity, and ultimately add to the species prospects of survival.

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Appendix 1

Field studies

Introduction

Field observations of *S. douglasi* were carried out in Bladensburg National Park, Winton, Queensland. This area consists of Mitchell-grass plains (Orr & Holmes 1994), the preferred habitat for *S. douglasi* (Lundie-Jenkins & Payne 2000). *S. Douglasi* has been abundant in this area previously (Misfud 2001).

Methods

Two field trials were conducted during five days, 16-21 July 2003, totaling 750 trap nights, and eight days, 13-21 March 2004, totaling 1944 trap nights. Small Elliot-traps baited with peanut butter, bacon and rolled oats were placed along two grids 100 x 100m with 10m between the traps, totalling 100 traps each, and a line transect running in a U shape with the sides 1000 / 500 / 1000m, traps every 50m totaling 50 traps. The traps were checked and re-baited daily just before sunrise (approximately 5am EST). Animals were brought back to Bladensburg Research Station (approximately 1 km from the field site), weighed, sexed and urine samples were collected before release at sunset (approximately 9pm EST) on the same day.

Results

The field observations showed a very low abundance of *S. douglasi*. Only two *S. douglasi*, both adult males, were caught over the entire period (Table 1). Two narrownosed planigales (*Planigale tenuirostris*) and one long-tailed planigale (*Planigale ingrami*) were the only other animals captured in the traps, aside from invertebrates.

Table 1. Trapping data for Bladensburg National Park July 2003 and March 2004.

Date	Species	Sex	Weight (g)	Urine sample	Comment
18 07 2003	*S. douglasi*	M	28	N/a	
19 03 2004	*P. tenuirostris*	M	7.0	N/a	
19 03 2004	*S. douglasi*	M	38.5	Possitive for sperm	
20 03 2004	*P. tenurostris*	M	N/a	N/a	Escaped
20 03 2004	*P. ingrami*	F	3.8	N/a	Dead

Discussion

Compared to previous trapping studies (Misfud 2001) the abundance of *S. douglasi* in Bladensburg national park was very low. This is cause for concern in regards to conservation of the species. The species is endangered (IUCN 1996) and the course for this classification stems from the restricted geographical spread of the species and the limited amount of suitable habitat (Lundie-Jenkins & Payne 2000). Specialist species like *S. douglasi* that live only in one particular habitat type have an increased likelihood of going extinct (Wilson, Dicman & Fletcher 2003). Thus, a decline in numbers in the area where the species has previously been abundant is undesirable. However, some new records of the species (Kutt 2003) have increased the distribution of *S. douglasi* to previously unknown places, which suggest that the species may be migrating into new areas. The reason for these large fluctuations in population size is unknown. It is possible that the severe climate changes that characterize this type of environment (Orr & Holmes 1984) cause variation in the density of *S. douglasi*, as resources are unpredictable (Morton 1978a;b).

The initial aim of the field study was to relate some of the findings in field to the main study of behaviour during different reproductive states in captivity. However, due to the small numbers of *S. douglasi* that were trapped, the field studies were not included in the main study. Nevertheless, there is scope for further research to continue study *S. douglasi* in field, to determine, for example, the reason for the large fluctuations in numbers of *S. douglas*i.

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Appendix 2

Appendix 2. Data of four female *S. douglasi*, July-November 2004, including weight, reproductive state, appetite and exercise-wheel running activity. Missing value=m.

						Exercice wheel			
Date	Female	State 1=oestrus, 0=non-oestrus	Weight (g)	Company s=single, m= male f=female	Food leftovers (g)	Distance (km)	Time (h:min:sec)	Average (km/h)	Max (km/h)
28/07/2004	F19	0	47.5	s	0	m	m	m	m
29/07/2004	F19	1	48	s	0	m	m	m	m
30/07/2004	F19	1	48.5	s	0	m	m	m	m
31/07/2004	F19	1	50	s	0	8.91	3:59:59	2.2	4.0
1/08/2004	F19	1	46.5	s	9	10.24	5:16:51	1.9	4.1
2/08/2004	F19	1	43.5	s	8	11.05	4:35:47	2.4	4.5
3/08/2004	F19	1	42	s	6	11.05	4:35:47	2.4	4.5
4/08/2004	F19	1	44	s	5	7.88	3:58:52	1.4	3.6
5/08/2004	F19	0	42.5	s	0	1.60	1:14:14	1.2	3.1
6/08/2004	F19	0	m	s	0	3.41	2:17:28	1.4	3.6
7/08/2004	F19	0	m	s	0	2.96	2:01:57	1.4	3.4
8/08/2004	F19	0	m	s	0	2.96	2:01:57	1.4	3.4
9/08/2004	F19	0	42.5	s	0	6.56	4:30:28	1.4	3.4
10/08/2004	F19	0	m	s	0	0.47	0:18:57	1.5	3.3
11/08/2004	F19	0	43	s	0	0.47	0:18:57	1.5	3.3
12/08/2004	F19	0	44.5	s	0	0.31	0:13:46	1.3	2.6
13/08/2004	F19	0	44	s	0	0.31	0:13:46	1.3	2.6
14/08/2004	F19	0	43.5	s	4	0.55	0:23:43	1.4	2.9
15/08/2004	F19	0	41.5	s	0	0.56	0:20:59	1.6	3.2
16/08/2004	F19	0	40.5	s	7.5	0.84	0:30:24	1.6	3.1
17/08/2004	F19	0	m	s	0	1.10	0:43:44	1.5	3.4
18/08/2004	F19	0	41.5	s	0	1.18	0:43:30	1.6	3.9

19/08/2004	F19	0	43	s	0	1.18	0:43:30	1.6	3.9
20/08/2004	F19	0	43	s	0	1.18	0:43:30	1.6	3.9
21/08/2004	F19	0	42.5	s	0	1.03	0:42:50	1.4	3.8
22/08/2004	F19	0	44	s	0	1.04	0:39:10	1.6	3.9
23/08/2004	F19	0	44.5	s	0	1.41	0:58:47	1.4	3.1
24/08/2004	F19	0	46	s	0	2.44	1:37:54	1.5	3.9
25/08/2004	F19	0	47.5	s	3.5	2.44	1:37:54	1.5	3.9
26/08/2004	F19	0	48	s	4.5	2.16	1:12:35	1.7	3.7
27/08/2004	F19	0	m	s	0	4.04	2:04:48	1.9	3.7
28/08/2004	F19	1	43	s	17	4.04	2:04:48	1.9	3.7
29/08/2004	F19	1	m	s	5	4.32	2:06:03	2.0	3.7
30/08/2004	F19	1	41.5	s	6	4.32	2:06:03	2.0	3.7
31/08/2004	F19	1	41.5	s	6.5	2.19	1:13:28	1.7	3.6
1/09/2004	F19	0	42.5	s	0	1.48	0:50:39	1.7	3.3
2/09/2004	F19	0	44	s	2	1.09	0:38:26	1.7	8.4
3/09/2004	F19	0	44.5	s	4	1.09	0:38:26	1.7	8.4
4/09/2004	F19	0	44.5	s	4.5	1.50	0:57:16	1.5	3.5
5/09/2004	F19	0	45	s	6	0.66	0:25:36	1.5	2.8
6/09/2004	F19	0	44.5	s	6	0.74	0:26:01	1.7	3.0
7/09/2004	F19	0	46.5	s	0	0.62	0:22:05	1.6	3.0
8/09/2004	F19	0	m	s	8	0.41	0:15:37	1.5	2.7
9/09/2004	F19	0	44	s	12.5	0.41	0:15:37	1.5	2.7
10/09/2004	F19	0	42.5	s	8	0.77	0:29:08	1.5	3.6
11/09/2004	F19	0	40	s	6	0.65	0:25:49	1.5	2.6
12/09/2004	F19	0	40.5	m	0	1.26	0:48:23	1.5	4.1
13/09/2004	F19	0	40.5	m	0	2.53	1:35:18	1.5	4.1
14/09/2004	F19	0	40	m	6	2.31	1:23:19	1.6	3.6
15/09/2004	F19	0	41	m	3	0.78	0:28:03	1.6	3.6
16/09/2004	F19	0	41	m	6	1.63	0:59:18	1.6	3.2
17/09/2004	F19	0	43	m	4	1.15	0:40:06	1.7	4.2

18/09/2004	F19	0	43.5	m	0	1.69	1:00:03	1.6	3.9
19/09/2004	F19	0	44.5	m	0	6.09	3:01:38	2.0	4.1
20/09/2004	F19	0	45.5	m	6	7.20	3:19:59	2.1	4.6
21/09/2004	F19	0	41.5	m	12	10.82	4:27:14	2.4	3.2
22/09/2004	F19	1	41.5	m	4.5	7.46	3:10:21	2.3	3.5
23/09/2004	F19	1	41.5	m	0	8.48	3:26:50	2.4	3.3
24/09/2004	F19	1	43	m	0	1.64	57:51:00	1.7	3.2
25/09/2004	F19	1	41	m	5	3.30	1:40:25	1.9	3.6
26/09/2004	F19	0	40.5	m	0	1.29	0:48:42	1.5	3.8
27/09/2004	F19	0	42	m	0	0.85	0:36:12	1.4	3.8
28/09/2004	F19	0	42.5	m	0	0.30	0:12:26	1.4	3.5
29/09/2004	F19	0	43	m	0	0.30	0:12:26	1.4	3.5
30/09/2004	F19	0	45.5	m	0	0.12	0:05:05	1.5	3.9
1/10/2004	F19	0	m	m	0	0.00	0:00:04	m	m
2/10/2004	F19	0	m	m	0	0.23	0:10:51	1.2	3.3
3/10/2004	F19	0	45.5	m	12	0.23	0:10:51	1.2	3.3
4/10/2004	F19	0	43	m	6.5	0.23	0:10:51	1.2	3.3
5/10/2004	F19	0	41	m	3	0.40	0:18:07	1.3	3.8
6/10/2004	F19	0	39.5	m	0	0.81	0:31:35	1.5	3.3
7/10/2004	F19	0	41	f	0	0.63	0:23:20	1.6	3.3
8/10/2004	F19	0	41.5	f	0	3.73	1:50:29	2.0	4.2
9/10/2004	F19	0	m	f	0	0.83	0:29:26	1.7	3.2
10/10/2004	F19	0	42.5	f	0	3.17	1:36:18	1.9	3.6
11/10/2004	F19	0	44	f	0	4.52	2:10:26	2.0	3.2
12/10/2004	F19	0	44	f	0	4.16	2:07:14	1.9	3.3
13/10/2004	F19	0	m	f	0	4.35	2:13:10	1.9	3.2
14/10/2004	F19	0	45.5	f	0	4.85	2:21:26	2.0	4.0
15/10/2004	F19	0	47.5	f	0	7.11	3:32:58	2.0	4.2
16/10/2004	F19	0	44.5	f	0	6.44	3:00:33	2.1	3.9
17/10/2004	F19	1	43	f	0	7.14	3:06:21	2.2	3.7

18/10/2004	F19	1	42	f	0	3.23	1:25:55	2.2	4.0
19/10/2004	F19	1	41.5	f	0	0.28	0:11:11	1.5	2.5
20/10/2004	F19	1	41.5	f	0	0.00	0	m	m
21/10/2004	F19	1	41	f	0	0.68	0:21:55	1.8	3.6
22/10/2004	F19	0	43	f	0	0.59	0:21:56	1.6	3.7
23/10/2004	F19	0	m	f	0	0.69	0:26:02	1.5	2.8
24/10/2004	F19	0	41.5	f	0	0.69	0:26:02	1.5	2.8
25/10/2004	F19	0	43	f	0	1.04	0:47:54	1.3	3.4
26/10/2004	F19	0	m	f	0	0.20	0:08:46	1.3	2.5
27/10/2004	F19	0	44.5	f	0	0.02	0:01:10	1.3	3.2
28/10/2004	F19	0	44.5	f	0	0.02	0:01:10	1.3	3.2
29/10/2004	F19	0	45	f	0	0.78	0:30:36	1.5	3.3
30/10/2004	F19	0	43	f	0	0.19	0:08:27	1.4	3.4
31/10/2004	F19	0	m	f	0	0.82	0:32:22	1.5	2.7
1/11/2004	F19	0	41	f	0	0.82	0:30:43	1.6	3.9
2/11/2004	F19	0	m	f	0	0.49	0:18:42	1.5	3.2
3/11/2004	F19	0	42.5	m	0	2.44	1:24:05	1.7	3.2
4/11/2004	F19	0	44	m	0	5.36	2:29:58	2.1	3.6
5/11/2004	F19	0	43.5	m	0	7.25	3:02:52	2.5	3.6
6/11/2004	F19	0	45	m	0	6.77	3:12:46	2.1	4.1
7/11/2004	F19	0	45	m	0	2.92	1:37:09	1.8	3.9
8/11/2004	F19	0	46	m	0	8.48	3:40:10	2.3	4.0
9/11/2004	F19	1	45.5	m	0	2.97	1:29:33	1.9	2.9
10/11/2004	F19	1	m	m	0	7.20	3:11:58	2.2	3.8
11/11/2004	F19	1	m	m	0	6.04	2:43:20	2.2	3.8
12/11/2004	F19	1	42.5	m	0	6.04	2:43:20	2.2	3.8
13/11/2004	F19	1	43	m	0	4.30	2:11:39	1.9	3.4
14/11/2004	F19	1	41.5	m	0	6.10	3:01:17	2.0	3.6
15/11/2004	F19	0	42.5	m	0	0.98	0:36:37	1.6	3.9
16/11/2004	F19	0	m	m	0	m	m	m	m

17/11/2004	F19	0	41.5	m	0	0.09	0:04:32	1.2	2.6
18/11/2004	F19	0	41.5	m	0	0.01	0:00:53	1.2	2.0
19/11/2004	F19	0	41.5	m	0	2.24	1:16:17	1.7	3.3
20/11/2004	F19	0	m	m	0	0.59	0:20:23	1.7	3.5
21/11/2004	F19	0	40	m	0	0.59	0:20:23	1.7	3.5
22/11/2004	F19	0	42.5	m	0	0.73	0:24:39	1.7	3.7
29/07/2004	F5	0	53.5	f	0	m	m	m	m
30/07/2004	F5	0	53.5	f	0	m	m	m	m
31/07/2004	F5	0	52.5	f	0	5.65	2:35:23	2.1	4.1
1/08/2004	F5	0	52.5	f	0	1.94	1:16:50	1.5	3.9
2/08/2004	F5	0	53.5	f	0	4.36	1:54:36	2.2	5.4
3/08/2004	F5	0	53	f	0	4.36	1:54:36	2.2	5.4
4/08/2004	F5	0	52.5	f	0	3.33	1:45:58	1.8	5.0
5/08/2004	F5	0	53	f	0	1.58	0:50:10	1.8	5.0
6/08/2004	F5	0	m	f	0	3.17	1:27:59	2.1	6.1
7/08/2004	F5	0	m	f	6.5	3.17	1:27:59	2.1	6.1
8/08/2004	F5	0	50	f	7	3.55	1:24:40	2.5	5.1
9/08/2004	F5	1	48	f	7.5	4.70	1:52:43	2.5	5.0
10/08/2004	F5	1	50	f	0	2.91	1:14:15	2.3	4.8
11/08/2004	F5	1	48	f	0	2.91	1:14:15	2.3	4.8
12/08/2004	F5	1	47.5	f	0	0.88	0:27:48	1.9	4.6
13/08/2004	F5	1	48	f	0	0.88	0:27:48	1.9	4.6
14/08/2004	F5	0	47.5	f	0	1.42	0:47:06	1.8	4.7
15/08/2004	F5	0	48	f	0	0.69	0:22:21	1.8	4.8
16/08/2004	F5	0	48	f	0	0.83	0:25:35	1.9	4.6
17/08/2004	F5	0	m	f	0	0.67	0:19:09	2.1	4.8
18/08/2004	F5	0	49	f	0	1.01	0:30:04	2.0	5.0
19/08/2004	F5	0	50.5	f	0	1.01	0:30:04	2.0	5.0
20/08/2004	F5	0	52.5	f	0	1.01	0:30:04	2.0	5.0
21/08/2004	F5	0	51	f	0	0.66	0:21:56	1.8	4.7

22/08/2004	F5	0	49.5	f	10	0.52	0:19:13	1.6	3.1
23/08/2004	F5	0	46.5	f	7	0.69	0:24:31	1.7	3.0
24/08/2004	F5	0	m	f	0	0.60	0:20:11	1.7	4.4
25/08/2004	F5	0	48.5	f	0	0.60	0:20:11	1.7	4.4
26/08/2004	F5	0	48.5	f	0	0.72	0:23:47	1.8	5.0
27/08/2004	F5	0	m	f	0	0.24	0:09:06	1.5	3.6
28/08/2004	F5	0	49	f	0	0.24	0:09:06	1.5	3.6
29/08/2004	F5	0	m	f	0	0.22	0:08:51	1.4	3.3
30/08/2004	F5	0	51.5	f	0	0.22	0:08:51	1.4	3.3
31/08/2004	F5	0	53	f	0	3.20	0:14:36	1.3	3.0
1/09/2004	F5	0	54.5	f	0	2.76	1:32:17	1.7	3.7
2/09/2004	F5	0	53	f	7	8.60	2:44:32	3.1	5.9
3/09/2004	F5	1	50.5	f	7.5	8.60	2:44:32	3.1	5.9
4/09/2004	F5	1	48.5	f	7	8.19	2:39:26	3.0	5.0
5/09/2004	F5	1	49.5	f	0	0.22	0:07:22	1.8	4.6
6/09/2004	F5	1	47.5	f	0	1.04	0:34:55	1.8	4.2
7/09/2004	F5	1	48	f	0	0.79	0:28:20	1.6	4.5
8/09/2004	F5	0	m	f	0	0.49	0:16:36	1.7	4.1
9/09/2004	F5	0	48	f	0	0.49	0:16:36	1.7	4.1
10/09/2004	F5	0	47	f	0	0.89	0:40:16	1.3	3.6
11/09/2004	F5	0	47	f	0	0.69	0:29:03	1.4	2.9
12/09/2004	F5	0	46.5	f	0	0.31	0:15:07	1.2	2.7
13/09/2004	F5	0	m	f	0	0.12	0:05:35	1.8	2.7
14/09/2004	F5	0	47	f	0	0.86	0:30:35	1.7	3.4
15/09/2004	F5	0	47	f	0	0.19	0:08:05	1.4	3.1
16/09/2004	F5	0	48	s	0	0.14	0:06:55	1.2	2.6
17/09/2004	F5	0	50	s	0	0.44	0:15:54	1.6	3.0
18/09/2004	F5	0	m	s	0	0.68	0:26:48	1.5	3.1
19/09/2004	F5	1	51.5	s	0	5.68	2:26:48	2.3	4.0
20/09/2004	F5	1	50.5	s	8	5.13	2:34:23	1.9	3.9

21/09/2004	F5	1	48.5	s	5	10.14	3:38:44	2.7	4.2
22/09/2004	F5	1	48.5	s	0	8.48	3:14:59	2.6	4.3
23/09/2004	F5	1	47.5	s	0	3.96	1:39:46	2.3	3.9
24/09/2004	F5	0	m	s	0	0.40	0:15:43	1.8	3.6
25/09/2004	F5	0	47	s	0	0.40	0:15:43	1.8	3.6
26/09/2004	F5	0	48.5	s	0	0.70	0:26:33	1.5	3.2
27/09/2004	F5	0	49	s	0	0.57	0:25:19	1.3	2.8
28/09/2004	F5	0	50	s	0	0.66	0:22:25	1.7	4.1
29/09/2004	F5	0	51	s	0	0.66	0:22:25	1.7	4.1
30/09/2004	F5	0	51.5	s	0	0.39	0:15:20	1.5	4.0
1/10/2004	F5	0	52.5	s	0	0.38	0:14:04	1.6	3.7
2/10/2004	F5	0	m	s	0	0.47	0:19:18	1.4	4.5
3/10/2004	F5	0	54	s	0	0.47	0:19:18	1.4	4.5
4/10/2004	F5	0	51	s	6.5	0.47	0:19:18	1.4	4.5
5/10/2004	F5	0	48.5	s	6	0.47	0:19:18	1.4	4.5
6/10/2004	F5	0	45	s	4	0.12	0:05:43	1.2	2.8
7/10/2004	F5	0	45.5	s	2	0.75	0:26:43	1.6	3.3
8/10/2004	F5	0	46	s	0	0.39	0:13:09	1.8	3.2
9/10/2004	F5	0	m	s	0	0.02	0:01:18	1.0	1.2
10/10/2004	F5	0	47	s	0	0.00	0:00:33	1.0	1.0
11/10/2004	F5	0	47	s	0	1.07	0:34:12	1.8	3.8
12/10/2004	F5	0	47	s	0	0.01	0:00:41	1.0	1.0
13/10/2004	F5	0	m	s	0	0.07	0:04:18	1.0	1.3
14/10/2004	F5	1	49.5	s	0	0.16	0:08:14	1.2	2.9
15/10/2004	F5	1	52	s	0	2.40	1:32:26	1.5	3.1
16/10/2004	F5	1	51.5	s	0	1.59	1:00:28	1.5	3.1
17/10/2004	F5	1	51	s	0	0.60	0:24:35	1.4	2.7
18/10/2004	F5	1	49	s	0	0.04	0:02:23	1.1	1.7
19/10/2004	F5	1	48.5	s	0	0.00	0	m	m
20/10/2004	F5	1	48	s	0	0.00	0	m	m

21/10/2004	F5	0	47	s	0	0.00	0	m	m
22/10/2004	F5	0	47	s	0	0.00	0	m	m
23/10/2004	F5	0	m	s	0	0.00	0	m	m
24/10/2004	F5	0	45.5	s	0	0.00	0	m	m
25/10/2004	F5	0	47	s	0	0.00	0	m	m
26/10/2004	F5	0	m	s	0	0.00	0	m	m
27/10/2004	F5	0	49	s	0	0.00	0	m	m
28/10/2004	F5	0	51.5	s	0	0.00	0	m	m
29/10/2004	F5	0	52.5	s	0	0.00	0	m	m
30/10/2004	F5	0	53	s	0	0.00	0	m	m
31/10/2004	F5	0	m	s	0	0.00	0	m	m
1/11/2004	F5	0	50.5	m	0	6.70	2:20:36	2.6	4.0
2/11/2004	F5	1	m	m	0	11.35	4:21:26	2.6	2.2
3/11/2004	F5	1	47.5	m	0	0.15	0:07:10	1.2	2.5
4/11/2004	F5	1	47	m	0	3.37	1:29:35	2.2	3.8
5/11/2004	F5	1	47	m	0	0.24	0:11:18	1.3	2.8
6/11/2004	F5	0	46	m	0	1.26	0:47:32	1.5	3.6
7/11/2004	F5	0	47.5	m	0	1.00	0:37:44	1.6	3.9
8/11/2004	F5	0	48	m	0	0.17	0:08:16	1.2	2.6
9/11/2004	F5	0	m	m	0	2.40	1:17:34	1.8	3.9
10/11/2004	F5	0	m	m	0	0.11	0:04:25	1.5	3.3
11/11/2004	F5	0	m	m	0	1.84	0:58:01	1.9	3.3
12/11/2004	F5	0	50.5	m	0	1.84	0:58:01	1.9	3.3
13/11/2004	F5	0	50	m	0	0.03	0:01:56	1.1	1.8
14/11/2004	F5	0	50	m	0	0.19	0:09:07	1.2	2.2
15/11/2004	F5	0	50	m	0	0.03	0:01:27	1.2	2.1
16/11/2004	F5	0	49	m	0	0.00	0:00:00	m	m
17/11/2004	F5	0	m	m	0	0.00	0:00:00	m	m
18/11/2004	F5	0	48.5	m	0	0.00	0:00:00	m	m
19/11/2004	F5	0	48	m	0	0.00	0:00:00	m	m

20/11/2004	F5	0	49	m	0	0.00	0:00:00	m	m
21/11/2004	F5	0	49	m	0	0.01	0:00:50	1.3	2.8
22/11/2004	F5	0	48.5	m	0	0.22	0:09:08	1.4	2.6
1/07/2004	G6	0	44	s	0	m	m	m	m
2/07/2004	G6	0	43.5	s	0	m	m	m	m
3/07/2004	G6	0	43.5	s	0	m	m	m	m
4/07/2004	G6	0	40.5	s	0	m	m	m	m
5/07/2004	G6	0	40	s	0	m	m	m	m
6/07/2004	G6	0	40	s	0	1.73	0:59:40	1.7	3.9
7/07/2004	G6	0	39.5	s	0	1.35	0:48:19	1.6	4.2
8/07/2004	G6	0	39.5	s	0	1.33	0:49:12	1.6	4.1
9/07/2004	G6	0	39.5	s	0	1.58	0:52:51	1.7	4.3
10/07/2004	G6	0	39	s	0	1.77	0:58:05	1.8	4.7
11/07/2004	G6	0	39	s	0	1.61	0:52:10	1.8	4.5
12/07/2004	G6	0	41	s	0	1.38	0:51:45	1.6	3.6
13/07/2004	G6	0	41	s	0	0.97	0:34:32	1.6	3.7
14/07/2004	G6	0	41.5	s	0	0.98	0:35:35	1.6	3.9
15/07/2004	G6	0	41	s	0	0.95	0:31:20	1.8	4.2
16/07/2004	G6	0	41	s	0	0.91	0:33:08	1.6	4.2
17/07/2004	G6	0	41	s	0	1.08	0:37:28	1.7	3.9
18/07/2004	G6	0	41	s	0	2.25	1:34:53	1.4	4.1
19/07/2004	G6	0	40.5	s	0	0.87	0:34:27	1.5	3.9
20/07/2004	G6	0	41	s	0	0.51	0:19:19	1.6	3.5
21/07/2004	G6	0	42	s	0	0.81	0:30:01	1.6	4.0
22/07/2004	G6	0	42	s	0	0.96	0:35:51	1.6	4.7
23/07/2004	G6	0	42.5	s	0	0.69	0:22:16	1.8	4.2
24/07/2004	G6	0	42.5	s	0	1.90	1:19:43	1.4	3.7
25/07/2004	G6	0	42.5	s	0	0.19	0:07:11	1.6	4.1
26/07/2004	G6	0	43.5	s	0	0.85	0:28:57	1.7	3.8
27/07/2004	G6	0	44.5	s	0	0.16	0:05:49	1.6	3.9

28/07/2004	G6	0	45	s	0	0.16	0:05:49	1.6	3.9
29/07/2004	G6	0	46.5	s	0	0.01	0:00:49	1.3	2.8
30/07/2004	G6	0	44.5	s	0	0.26	0:09:30	1.6	4.2
31/07/2004	G6	1	44	s	0	0.01	0:00:39	1.2	2.1
1/08/2004	G6	1	43.5	s	0	0.00	0:00:05	1.0	1.0
2/08/2004	G6	1	43.5	s	0	0.01	0:00:19	1.0	1.0
3/08/2004	G6	1	44	s	0	0.01	0:00:19	1.0	1.0
4/08/2004	G6	1	43.5	s	0	0.00	0:00:09	1.0	1.0
5/08/2004	G6	1	43	s	0	0.00	0:00:11	1.0	1.0
6/08/2004	G6	0	43	s	0	0.00	0:00:03	1.0	1.0
7/08/2004	G6	0	m	s	0	0.00	0	m	m
8/08/2004	G6	0	m	s	0	m	m	m	m
9/08/2004	G6	0	44	s	0	0.00	0:00:09	1.1	2.2
10/08/2004	G6	0	m	s	0	0.00	0:00:09	1.1	2.2
11/08/2004	G6	0	45.5	s	0	0.00	0:00:09	1.1	2.2
12/08/2004	G6	0	45	s	0	0.22	0:07:30	1.7	3.1
13/08/2004	G6	0	43	s	0	0.22	0:07:30	1.7	3.1
14/08/2004	G6	0	42	s	3	0.30	0:10:41	1.7	3.6
15/08/2004	G6	0	43	s	0	1.01	0:31:17	1.9	4.5
16/08/2004	G6	0	43	s	0	1.29	0:35:54	1.2	4.4
17/08/2004	G6	0	m	s	0	2.43	1:20:54	1.8	4.3
18/08/2004	G6	0	45.5	s	0	1.36	0:41:36	1.9	4.2
19/08/2004	G6	0	44.5	s	0	2.04	1:04:26	1.8	3.8
20/08/2004	G6	0	45	s	0	2.04	1:04:26	1.8	3.8
21/08/2004	G6	0	44.5	s	0	0.90	0:26:44	2.0	3.8
22/08/2004	G6	0	46.5	s	0	0.20	0:06:52	1.8	3.2
23/08/2004	G6	0	47.5	s	0	0.86	1:31:50	1.6	3.7
24/08/2004	G6	1	45	s	7	3.87	1:51:47	2.0	4.1
25/08/2004	G6	1	44.5	s	3.5	3.87	1:51:47	2.0	4.1
26/08/2004	G6	1	44	s	0	6.13	2:32:30	2.4	4.1

27/08/2004	G6	1	m	s	0	3.42	1:28:57	2.3	3.7
28/08/2004	G6	1	43	s	0	3.42	1:28:57	2.3	3.7
29/08/2004	G6	1	m	s	0	1.28	0:38:58	1.9	4.0
30/08/2004	G6	1	44.5	s	0	1.28	0:38:58	1.9	4.0
31/08/2004	G6	0	44.5	s	0	0.23	0:10:00	1.4	3.8
1/09/2004	G6	0	45	s	0	0.37	0:13:13	1.6	3.7
2/09/2004	G6	0	m	s	4	0.32	0:11:14	1.6	5.2
3/09/2004	G6	0	44.5	s	0	0.32	0:11:14	1.6	5.2
4/09/2004	G6	0	45	s	0	0.06	0:02:12	1.6	6.0
5/09/2004	G6	0	46	s	3	0.39	0:14:38	1.6	3.5
6/09/2004	G6	0	46	s	6	0.32	0:13:16	1.4	3.0
7/09/2004	G6	0	42.5	s	7	0.37	0:13:51	1.6	3.2
8/09/2004	G6	0	m	s	6	0.29	0:10:13	1.7	4.2
9/09/2004	G6	0	41.5	s	4	0.29	0:10:14	1.7	4.2
10/09/2004	G6	0	41.5	m	3.5	0.87	0:29:58	1.7	4.3
11/09/2004	G6	0	41	m	0	m	m	m	m
12/09/2004	G6	0	41	m	0	m	m	m	m
13/09/2004	G6	0	m	m	0	m	m	m	m
14/09/2004	G6	0	41.5	m	0	m	m	m	m
15/09/2004	G6	0	42.5	m	0	m	m	m	m
16/09/2004	G6	0	43	m	0	m	m	m	m
17/09/2004	G6	0	44	m	0	0.95	0:25:11	2.2	4.6
18/09/2004	G6	0	47	m	0	1.13	0:34:35	1.9	3.9
19/09/2004	G6	0	48	m	0	0.01	0:00:19	2.0	3.4
20/09/2004	G6	0	47	m	8	0.01	0:00:19	2.0	3.4
21/09/2004	G6	0	45	m	6	0.00	0	m	m
22/09/2004	G6	1	45	m	7	0.00	0	m	m
23/09/2004	G6	1	41.5	m	0	m	m	m	m
24/09/2004	G6	1	40	m	0	m	m	m	m
25/09/2004	G6	1	41	m	0	0.00	0	m	m

26/09/2004	G6	1	42	m	0	0.00	0	m	m
27/09/2004	G6	1	43	m	0	0.00	0	m	m
28/09/2004	G6	0	41.5	m	0	m	m	m	m
29/09/2004	G6	0	42.5	m	0	0.00	0	m	m
30/09/2004	G6	0	m	m	0	0.00	0	m	m
1/10/2004	G6	0	m	m	0	0.00	0	m	m
2/10/2004	G6	0	m	m	0	0.00	0	m	m
3/10/2004	G6	0	44.5	m	0	0.00	0	m	m
4/10/2004	G6	0	45	m	0	0.00	0	m	m
5/10/2004	G6	0	44.5	m	0	0.00	0	m	m
6/10/2004	G6	0	41	m	5	0.00	0	m	m
7/10/2004	G6	0	42.5	f	0	0.00	0	m	m
8/10/2004	G6	0	43.5	f	0	0.00	0	m	m
9/10/2004	G6	0	m	f	0	0.00	0	m	m
10/10/2004	G6	0	43.5	f	0	0.01	0:00:18	2.7	3.1
11/10/2004	G6	0	45.5	f	0	0.07	0:01:56	2.3	4.0
12/10/2004	G6	0	45	f	0	0.15	0:03:50	2.3	4.5
13/10/2004	G6	0	m	f	0	0.00	0	m	m
14/10/2004	G6	0	45.5	f	0	0.00	0	m	m
15/10/2004	G6	0	47	f	0	0.15	0:04:02	2.2	5.0
16/10/2004	G6	0	48.5	f	0	0.07	0:01:49	2.3	4.1
17/10/2004	G6	0	48.5	f	0	0.00	0	m	m
18/10/2004	G6	1	47	f	8	0.00	0	m	m
19/10/2004	G6	1	44.5	f	8	0.01	0:00:36	1.8	3.4
20/10/2004	G6	1	m	f	4	0.00	0	m	m
21/10/2004	G6	1	43.5	f	0	0.00	0	m	m
22/10/2004	G6	1	42.5	f	0	0.00	0	m	m
23/10/2004	G6	1	m	f	0	0.00	0	m	m
24/10/2004	G6	0	43	f	0	0.00	0	m	m
25/10/2004	G6	0	45	f	0	0.00	0	m	m

26/10/2004	G6	0	44.5	f	0	0.00	0	m	m
27/10/2004	G6	0	45	f	0	0.00	0	m	m
28/10/2004	G6	0	45	f	0	0.00	0	m	m
29/10/2004	G6	0	45	f	0	0.00	0	m	m
30/10/2004	G6	0	48	f	0	0.00	0	m	m
31/10/2004	G6	0	m	f	0	0.00	0	m	m
1/11/2004	G6	0	44	f	0	0.00	0	m	m
2/11/2004	G6	0	42	m	0	0.00	0	m	m
3/11/2004	G6	0	42	m	0	0.00	0	m	m
4/11/2004	G6	0	42.5	m	0	0.00	0	m	m
5/11/2004	G6	0	43	m	0	0.00	0	m	m
6/11/2004	G6	0	43	m	0	0.00	0	m	m
7/11/2004	G6	0	42.5	m	0	0.00	0	m	m
8/11/2004	G6	0	44.5	m	0	0.00	0	m	m
9/11/2004	G6	0	m	m	0	0.01	0:00:34	m	m
10/11/2004	G6	0	45	m	0	0.00	0	m	m
11/11/2004	G6	0	m	m	0	0.00	0	m	m
12/11/2004	G6	0	45	m	0	0.00	0	m	m
13/11/2004	G6	1	48	m	0	0.00	0	m	m
14/11/2004	G6	1	43	m	0	0.00	0	m	m
15/11/2004	G6	1	m	m	0	0.00	0	m	m
16/11/2004	G6	1	41	m	0	0.00	0	m	m
17/11/2004	G6	1	42.5	m	0	0.00	0	m	m
18/11/2004	G6	1	42.5	m	0	0.00	0	m	m
19/11/2004	G6	0	42.5	m	0	0.00	0	m	m
20/11/2004	G6	0	m	m	0	0.00	0	m	m
21/11/2004	G6	0	42	m	0	0.00	0	m	m
22/11/2004	G6	0	43	m	0	0.00	0	m	m
1/07/2004	G7	0	44.5	s	0	m	m	m	m
2/07/2004	G7	0	43.5	s	0	m	m	m	m

3/07/2004	G7	0	44	s	0	m	m	m	m
4/07/2004	G7	1	41.5	s	8	m	m	m	m
5/07/2004	G7	1	41	s	1.5	m	m	m	m
6/07/2004	G7	1	40	s	0	11.30	4:15:50	2.6	4.8
7/07/2004	G7	1	40	s	0	5.62	2:52:15	1.9	4.7
8/07/2004	G7	1	38.5	s	0	1.90	1:23:53	1.3	4.5
9/07/2004	G7	1	39	s	0	0.96	0:36:29	1.5	4.0
10/07/2004	G7	0	38	s	0	1.44	1:04:17	1.3	4.4
11/07/2004	G7	0	40	s	0	1.78	1:20:47	1.3	4.4
12/07/2004	G7	0	41	s	0	0.32	0:11:06	3.7	3.8
13/07/2004	G7	0	41.5	s	0	0.56	0:20:20	1.6	3.9
14/07/2004	G7	0	42	s	0	0.56	0:20:20	1.6	3.9
15/07/2004	G7	0	42	s	0	0.29	0:09:28	1.8	4.4
16/07/2004	G7	0	43	s	0	0.40	0:14:05	1.7	4.1
17/07/2004	G7	0	43	s	0	0.35	0:11:31	1.8	4.0
18/07/2004	G7	0	45	s	0	0.31	0:10:12	1.8	4.2
19/07/2004	G7	0	m	s	0	0.11	0:03:40	1.9	4.0
20/07/2004	G7	0	m	s	0	0.14	0:04:13	2.0	4.4
21/07/2004	G7	0	44	m	0	0.20	0:07:01	1.7	3.5
22/07/2004	G7	0	43.5	m	0	1.84	1:05:34	1.6	4.2
23/07/2004	G7	0	43	m	0	0.65	0:23:01	1.6	4.0
24/07/2004	G7	0	m	m	0	2.93	1:31:50	1.9	4.5
25/07/2004	G7	0	43.5	m	0	0.97	0:32:37	1.7	3.7
26/07/2004	G7	0	44.5	m	0	0.81	0:35:02	1.3	3.3
27/07/2004	G7	0	44.5	m	0	1.64	1:03:53	1.5	3.6
28/07/2004	G7	0	45.5	m	0	1.11	0:40:46	1.6	3.7
29/07/2004	G7	0	46.5	m	0	1.18	0:46:14	1.5	3.7
30/07/2004	G7	1	47	m	0	3.14	1:42:35	1.8	4.2
31/07/2004	G7	1	44.5	m	4	5.22	2:35:43	2.0	4.9
1/08/2004	G7	1	m	m	0	5.97	2:53:13	2.0	4.3

2/08/2004	G7	1	42.5	m	0	2.89	1:20:46	2.1	4.0
3/08/2004	G7	1	42	m	0	2.89	1:20:46	2.1	4.0
4/08/2004	G7	0	42	m	0	0.88	0:32:23	1.6	3.5
5/08/2004	G7	0	42	m	0	0.41	0:15:13	1.6	3.4
6/08/2004	G7	0	43	m	0	0.68	0:23:57	1.7	4.3
7/08/2004	G7	0	m	m	0	0.79	0:31:52	1.5	3.4
8/08/2004	G7	0	m	m	0	1.13	0:48:27	1.4	3.5
9/08/2004	G7	0	40.5	m	0	0.47	0:20:57	1.3	3.7
10/08/2004	G7	0	m	m	0	0.71	0:27:26	1.5	3.8
11/08/2004	G7	0	42.5	m	0	0.71	0:27:26	1.5	3.8
12/08/2004	G7	0	42.5	m	0	0.60	0:24:16	1.4	3.6
13/08/2004	G7	0	44	m	0	0.60	0:24:16	1.4	3.6
14/08/2004	G7	0	46.5	m	0	0.67	0:28:59	1.4	3.7
15/08/2004	G7	0	46.5	m	0	1.24	0:47:52	1.5	3.2
16/08/2004	G7	0	44.5	m	7.5	4.37	2:23:29	1.8	4.6
17/08/2004	G7	0	42.5	m	11	8.34	3:13:53	2.5	3.9
18/08/2004	G7	1	40	m	9	8.61	3:37:14	2.3	4.7
19/08/2004	G7	1	40	m	0	4.62	2:00:14	2.3	4.3
20/08/2004	G7	1	40	m	0	4.62	2:00:14	2.3	4.3
21/08/2004	G7	1	41	m	0	1.45	0:46:32	1.8	3.8
22/08/2004	G7	0	41	m	0	1.41	0:49:01	1.7	3.6
23/08/2004	G7	0	41	m	0	1.41	0:49:01	1.7	3.6
24/08/2004	G7	0	m	m	0	1.77	1:09:51	1.5	3.6
25/08/2004	G7	0	44.5	m	0	1.77	1:09:51	1.5	3.6
26/08/2004	G7	0	45	m	0	0.66	0:26:19	1.5	3.0
27/08/2004	G7	0	m	m	0	0.82	0:30:58	1.5	3.7
28/08/2004	G7	0	45.5	m	0	0.82	0:30:58	1.5	3.7
29/08/2004	G7	0	m	m	0	1.16	0:39:11	1.7	3.9
30/08/2004	G7	0	45	m	7	1.16	0:39:11	1.7	3.9
31/08/2004	G7	0	42.5	m	11	0.63	0:23:28	1.6	4.0

1/09/2004	G7	0	40	m	10.5	0.31	0:10:31	1.7	3.3
2/09/2004	G7	0	41	m	7	0.52	0:18:47	1.6	6.3
3/09/2004	G7	0	41.5	f	5	0.52	0:18:47	1.6	6.3
4/09/2004	G7	0	42.5	f	8.5	2.40	1:23:41	1.7	4.6
5/09/2004	G7	0	42	f	0	2.76	1:32:00	1.8	4.7
6/09/2004	G7	0	43.5	f	0	3.33	1:34:30	2.1	4.3
7/09/2004	G7	0	44.2	f	0	3.53	1:40:21	2.1	4.3
8/09/2004	G7	0	45	f	0	1.86	0:59:56	1.8	4.5
9/09/2004	G7	0	46	f	0	1.86	0:59:56	1.8	4.5
10/09/2004	G7	0	47	f	0	2.24	1:11:06	1.8	4.0
11/09/2004	G7	1	46.5	f	6	7.22	3:30:01	2.0	4.2
12/09/2004	G7	1	m	f	6	7.86	3:25:49	2.2	4.6
13/09/2004	G7	1	m	f	0	9.59	3:47:56	2.5	4.9
14/09/2004	G7	1	43	f	0	5.82	2:27:39	2.3	4.1
15/09/2004	G7	1	43	f	0	4.90	2:16:16	2.1	4.4
16/09/2004	G7	1	43	f	0	3.01	1:41:15	1.7	4.0
17/09/2004	G7	1	43	f	0	2.22	1:22:36	1.6	4.1
18/09/2004	G7	0	43	f	0	1.87	1:09:58	1.6	4.3
19/09/2004	G7	0	43.5	f	0	1.61	0:59:50	1.6	4.2
20/09/2004	G7	0	44.5	f	0	2.10	1:15:46	1.6	4.6
21/09/2004	G7	0	m	f	0	3.13	1:35:52	1.9	4.3
22/09/2004	G7	0	44	f	0	1.30	0:47:27	1.6	4.3
23/09/2004	G7	0	44.5	f	0	3.26	1:41:40	1.9	4.5
24/09/2004	G7	0	m	f	0	1.31	0:50:51	1.5	4.1
25/09/2004	G7	0	m	f	0	1.31	0:50:51	1.5	4.1
26/09/2004	G7	0	48	f	0	1.31	0:46:04	1.7	3.7
27/09/2004	G7	0	51	f	0	0.63	0:23:12	1.6	3.6
28/09/2004	G7	0	49	f	0	1.34	0:37:02	2.1	9.4
29/09/2004	G7	1	46	f	0	1.34	0:37:02	2.1	9.4
30/09/2004	G7	1	43.5	f	0	7.07	3:05:08	2.2	4.6

1/10/2004	G7	1	43	f	0	6.03	2:31:53	2.3	4.4
2/10/2004	G7	1	m	f	0	1.87	0:58:26	1.9	4.3
3/10/2004	G7	1	44	f	0	1.87	0:58:26	1.9	4.3
4/10/2004	G7	0	43.5	f	0	1.87	0:58:26	1.9	4.3
5/10/2004	G7	0	44	f	0	0.43	0:17:36	1.4	2.6
6/10/2004	G7	0	45	f	0	0.66	0:23:59	1.6	3.5
7/10/2004	G7	0	44	s	0	1.59	0:53:29	1.7	4.0
8/10/2004	G7	0	44	s	0	1.31	0:44:46	1.7	4.0
9/10/2004	G7	0	m	s	0	0.04	0:01:38	1.6	3.6
10/10/2004	G7	0	45.5	s	0	0.00	0	0.0	0.0
11/10/2004	G7	0	46.5	s	0	0.00	0	0.0	0.0
12/10/2004	G7	0	46	s	0	0.00	0	0.0	0.0
13/10/2004	G7	0	m	s	0	0.00	0	0.0	0.0
14/10/2004	G7	0	40	s	0	0.01	0:00:26	1.9	3.7
15/10/2004	G7	0	39.5	s	0	0.00	0	0.0	0.0
16/10/2004	G7	0	41.5	s	0	0.00	0	0.0	0.0
17/10/2004	G7	0	44.5	s	0	1.63	0:47:21	2.0	3.6
18/10/2004	G7	0	43	s	0	0.96	0:36:15	1.5	3.2
19/10/2004	G7	0	44	s	0	0.35	0:13:04	1.6	3.2
20/10/2004	G7	0	43	s	0	1.30	0:43:43	1.7	2.6
21/10/2004	G7	0	43.5	s	0	0.22	0:12:12	1.0	1.8
22/10/2004	G7	0	45.5	s	0	0.40	0:17:48	1.3	2.5
23/10/2004	G7	0	m	s	0	2.66	1:24:28	1.8	4.0
24/10/2004	G7	0	46.5	s	0	2.66	1:24:28	1.8	4.0
25/10/2004	G7	1	45.5	s	0	10.82	4:26:44	2.4	7.6
26/10/2004	G7	1	44.5	s	0	2.66	1:24:31	1.8	3.7
27/10/2004	G7	1	42.5	s	0	0.43	0:15:51	1.6	2.7
28/10/2004	G7	1	43	s	9	0.00	0:00:07	2.1	3.5
29/10/2004	G7	0	43	s	12	0.00	0:00:07	2.1	3.5
30/10/2004	G7	0	43	s	10	2.74	1:14:31	2.2	3.8

31/10/2004	G7	0	m	s	0	0.76	0:29:40	1.5	3.3
1/11/2004	G7	0	43	s	0	0.71	0:28:16	1.5	3.5
2/11/2004	G7	0	m	s	0	0.38	0:14:23	1.6	3.0
3/11/2004	G7	0	43.5	s	0	0.43	0:16:23	1.5	3.0
4/11/2004	G7	0	44	s	0	0.37	0:17:19	1.2	3.4
5/11/2004	G7	0	43.5	m	0	1.20	0:44:45	1.6	3.7
6/11/2004	G7	0	46	m	0	0.57	0:22:53	1.5	3.3
7/11/2004	G7	0	48	m	6	1.83	0:51:15	2.1	4.0
8/11/2004	G7	1	m	m	5	3.01	1:23:16	2.1	4.0
9/11/2004	G7	1	44	m	0	5.44	2:22:55	2.2	4.2
10/11/2004	G7	1	44	m	0	3.38	1:36:47	2.0	2.9
11/11/2004	G7	1	m	m	0	2.32	1:08:24	2.0	4.0
12/11/2004	G7	0	40	m	3	2.32	1:08:24	2.0	4.0
13/11/2004	G7	0	41	m	0	3.85	1:42:49	2.2	3.9
14/11/2004	G7	0	41	m	8	3.95	1:47:40	2.2	3.9
15/11/2004	G7	0	40.5	m	9	0.00	0:00:27	1.0	1.1
16/11/2004	G7	0	41	m	0	0.00	0:00:27	1.0	1.0
17/11/2004	G7	0	40.5	m	0	0.00	0:00:27	1.0	1.0
18/11/2004	G7	0	42.5	m	0	0.21	0:11:58	1.0	2.5
19/11/2004	G7	0	41.5	m	0	0.01	0:00:39	1.1	1.5
20/11/2004	G7	0	m	m	0	0.01	0:00:41	1.0	1.1
21/11/2004	G7	0	44	m	0	0.01	0:00:41	1.0	1.1
22/11/2004	G7	0	44.5	m	0	0.00	0:00:31	1.0	1.0