Ecophysiology of feral cats (*Felis catus*) in Australia

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Don’t dream your life, live your dream!!

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List of abbreviations

BMR	Basal metabolic rate
GPS	Global positioning system
M_b	Body mass
MR	Metabolic rate
STPD	At standard temperature, pressure and dry conditions
SD	Standard derivation
SE	Standard error
T_a	Ambient temperature
T_b	Body temperature
Temp	temperate
TNZ	Thermal neutral zone
Vic.	Victoria
WA	Western Australia

Projektzusammenfassung

Die verwilderte Hauskatze (*Felis catus*) kommt weltweit in allen vom Menschen besiedelten Gebieten vor. In Australien und auf zahlreichen Inseln weltweit haben Katzen entscheidend zur Ausrottung einheimischer Tierarten beigetragen und werden für das Scheitern von Wiedereinbürgerungsversuchen einheimischer bedrohter Arten verantwortlich gemacht. Katzen sind in der Lage, sich auch unter extremen Bedingungen (unvorhersagbare Regenfälle und Nahrungsverfügbarkeit, Extremtemperaturen) in nahezu jedem Lebensraum äußerst erfolgreich auszubreiten. Die Grundlagen dieser extremen Anpassungsfähigkeit sind derzeit noch nicht vollständig geklärt, es wird jedoch angenommen, dass eine Vielzahl verschiedener Faktoren (z.B. Physiologie und Verhalten), für den Erfolg als invasive Art verantwortlich gemacht werden können. Die hier vorliegende Doktorarbeit befasst sich mit den verschiedenen potentiell möglichen physiologischen Anpassungsfähigkeiten bezüglich verschiedener Klimazonen, Jahreszeiten, Inselisolation und Gefangenschaft. Hierfür werden der Energiehaushalt (basale Stoffwechselrate, BMR), Körpermasse sowie Temperaturregulation verwilderter Hauskatzen aus verschiedensten Lebensräumen Australiens untersucht und miteinander verglichen. Unter anderem wird untersucht, ob Katzen durch eine reduzierte Basalstoffwechselrate an extreme Bedingungen (z.B. aride Klimazonen) angepasst sind bzw. eine Präadaptation vorliegt. Ergänzend zu einer möglicherweise auftretenden physiologischen Anpassungsfähigkeit wird außerdem eine besondere Verhaltensanpassung an ein semiarides Inselhabitat postuliert und ebenfalls in der vorliegenden Arbeit untersucht.

Die ersten drei Kapitel beschreiben den Ablauf sowie Ergebnisse von Messungen im Feld. Es werden Stoffwechsel, Körpermasse sowie Aktivität und Körpertemperatur von Katzen verschiedener

Habitate verglichen, die nur kurze Zeit (ein bis zwei Tage) in Gefangenschaft gehalten wurden. Diese Vorgehensweise war die beste Möglichkeit, physiologische Anpassung an Lebensraum und Jahreszeit der Katzen zu messen, ohne diese physiologischen Parameter durch Gefangenschaft zu beeinflussen.

Kapitel 4 und 5 untersuchen und diskutieren die Auswirkungen der Gefangenschaft (12 Monate) auf zwei physiologische Parameter: der Basalstoffwechselrate und den Körpertempertuarzyklus.

Das 6. Kapitel beschreibt Untersuchungen zur Verhaltensanpassung der Katze. In diesem Zusammenhang werden Territoriumsgrösse, Überlappung der Territorien und Aktivitätsmuster einer semiariden Inselkatzenpopulation untersucht.

Kapitel 1 vergleicht die Basalstoffwechselrate von Katzenpopulationen aus verschiedenen Klimazonen (aride und gemässigte Zone) sowie Jahreszeiten (Sommer und Winter). Der Stoffwechsel jedes Individuums wurde noch am Tag des Fanges einmal in ihrer Thermoneutralzone (28-30 ^{o}C) gemessen. Die Ergebnisse zeigen keine Anpassung des Stoffwechsels an verschiedene Klimazonen (P = 0.365), jedoch weisen Katzen im Sommer einen 25% reduzierten Basalstoffwechel im Vergleich zum Winter auf (P = 0.049). Dieser Unterschied kann durch verschiede Beuteabundanzen, sowie mit dem Beginn der Fortpflanzungszeit erklärt werden. Im Winter sind Reptilien, Amphibien und auch Insekten weniger aktiv, und Katzen müssen daher längere Zeit für ihre Beutesuche investieren, um ihren Energiebedarf zu decken. Darüberhinaus werden Katzen zu Beginn der Winterzeit Fortpflanzungspartner suchen. Diese Punkte können zu einer Vergrößerung des Territoriums sowie Erhöhung der Aktivität führen, woraus wiederum eine Erhöhung der basalen Stoffwechselrate resultieren könnte.

Die vorliegende Arbeit vergleicht des Weiteren die Masse verwilderter Hauskatzen aus verschiedenen Klimazonen sowie Insel- und Festlandpopulationen miteinander (Kapitel 2). Es wurde ein signifikant niedrigeres Körpermassenspektrum von Katzen aus tropischen Inseln im Vergleich zu allen anderen untersuchten Katzen gefunden ($P < 0.0001$). Der Grund für das gefundene Ergebnis ist vermutlich auf ein nährstoffarmes Nahrungsangebot auf diesen Inseln zurückzuführen. Dieses Nahrungsangebot könnte möglicherweise die Körperentwicklung im jungen Katzenalter beeinträchtigen, was wiederum in einem kleineren und leichteren Körper resultiert.

Kapitel 3 untersucht die Wechselbeziehung von Körpertemperatur und Aktivität von freilaufenden (free-ranging) verwilderten Hauskatzen. Dafür wurde ein Globales Positionsbestimmungssystem (GPS) benutzt. Die GPS- Halsbänder erfassten in Zeitintervallen von 10 Minuten einen Positionspunkt (in geographischen Längen- und Breiten) der Katze. Als Aktivität definiert wurde die Entfernung, welche die Katze innerhalb der 10 Minuten zurücklegte. Ergänzend wurden Körpertemperaturlogger in die Bauchhöhle der Katzen implantiert, die ebenfalls in Intervallen von 10 Minuten einen Körpertemperaturwert in Echtzeit, aufzeichneten. Beide Zyklen, Körpertemperatur und Aktivität, weisen eine nachtaktive Eigenschaft auf, mit höheren Werten während der Nachtphase. Außerdem zeigen die Ergebnisse, dass die Tageszeit den stärksten Einfluss auf den Körpertemperaturzyklus hat. Dies ist vermutlich auf einen endogenen Zyklus der Körpertemperatur zurückzuführen. Weiterhin zeigen die Ergebnisse, dass die Körpertemperatur (Amplitude) durch Aktivität verändert werden kann was durch Körperwärmeerhöhung bei Bewegung zu erklären ist. Dieser Effekt wird besonders in der inaktiven Phase am Tag deutlich, da eine niedrigere Körperbasistemperatur durch Aktivität stärker ansteigt als in der aktiven Nachtphase mit höherer Basiskörpertemperatur. Die vorliegende Studie zeigt jedoch auch, dass man den endogenen Körpertemperaturzyklus nicht mit dem Aktivitätenzyklus gleichsetzen kann, da beide Datensätze nur geringfügig synchronisiert sind.

Kapitel 4 beschreibt die Auswirkung der Gefangenschaft auf zwei physiologische Parameter: Basalstoffwechselrate (BMR) und Körpertemperaturzyklus. Es wurden verwilderte Hauskatzen gefangen und für ein Jahr in Aussengehegen am Forschungszentrum in Perth gehalten. Die Katzen wurden einmal täglich gefüttert, hatten darüber hinaus jedoch keinen Kontakt zu Menschen, da eine Gewöhnung an den Menschen vermieden werden sollte. Die Basalstoffwechselrate wurde zu zwei Zeitpunkten, nach sechs Monaten sowie nach 12 Monaten Haltung in Gefangenschaft bestimmt. Diese Werte zeigen, dass die BMR von in Gefangenschaft lebenden Katzen im Vergleich zu freilebenden Katzen sich im Laufe eines Jahres in Gefangenschaft um 36% verringert ($P < 0.01$). Diese Verringerung des BMR könnte mit einer Verdopplung des Körperfettanteils erklärt werden. Der Körperfettanteil der frei lebenden (N= 5) sowie der in Gefangenschaft lebenden Katzen (N= 6) wurde durch eine Soxleth Extraktion ermittelt. Es zeigte sich eine Verdopplung des Körperfetts von 7 auf 14% der in Gefangenschaft lebenden Katzen. Die Verdopplung des Körperfetts, verbunden mit einem stoffwechselträgeren Fettgewebe im Vergleich zu Muskelgewebe könnte eine Erklärung für den oben erwähnten um 36 Prozent verringerten Stoffwechsel der gefangenen Katzen sein. Eine zweite Hypothese für den reduzierten Stoffwechsel ist die Änderung der Nahrung in Gefangenschaft, und eine daraus resultierende Verkürzung des sehr stoffwechselaktiven Darmtraktes. Katzen in Gefangenschaft wurden mit Katzenfutter oder Fisch gefüttert, beides sehr gut verdauliche Nahrungsmittel. Die Nahrung freilebender Katzen andererseits besteht aus verschiedenen Beutetieren, wie Säugetieren, Vögeln, Reptilien, aber auch Grasshüpfern (Gomphocerinae sp), Käfern (Coleoptera sp.) und anderen schwerverdaulichen Insekten. Möglicherweise ist durch diesen Nahrungsunterschied der Darmtrakt der freilebenden Katzen länger als bei Katzen in Gefangenschaft, da schwerverdauliche Insekten längere Zeit im Darm verweilen müssen, um aufgespalten zu werden. Bei Katzen in Gefangenschaft wären eine Verkürzung des Darmtrakts und damit eine reduzierte Stoffwechselaktivität durch zuverlässig, leicht verdauliche Kost möglich. Diese Hypothese müsste durch weiterführende Studien untersucht werden.

Der Körpertemperaturzyklus wildlebender Katzen zeigt einen ausgeprägten nachtaktiven Rhythmus mit höheren T_b-Werten während der Nacht, welche zum Ende der Nachtphase sinken und niedriger sind als am Tag. Dieser Zyklus verändert sich, wenn Katzen in Gefangenschaft gehalten werden. Der ausgeprägte Tag-Nacht Zyklus, der in der vorliegenden Arbeit bei wildlebenden Katzen gefunden wurde, ist bei gefangenen Katzen nicht mehr sichtbar. Weiterhin zeigen die Daten eine Verschiebung des Körpertemperturpeaks, von Mitternacht (freilaufende Katzen) zum Mittag (12:00-16:00 Uhr, Katzen in Gefangenschaft). Dieses Phänomen kann mit der Veränderung der Lebensumstände in Gefangenschaft erklärt werden: Die gefangenen Katzen wurden täglich zwischen 12:00 und 16:00 Uhr gefüttert und hatten zudem eine sehr begrenzte soziale Interaktion mit Artgenossen. Territoriumskämpfe, Partnersuche und auch das Jagen der Beute waren bei diesen Katzen nicht gegeben. Die Ergebnisse des 4. Kapitels zeigen eindrücklich, wie Gefangenschaft die Stoffwechsel- und circadiane Physiologie der verwilderten Hauskatze beeinflusst.

In Kapitel 5 werden die Ergebnisse der Stoffwechseluntersuchungen dieser Arbeit (Kapitel 1 und 4), mit der aktuellsten Stoffwechselstudie verschiedener Arten der Ordnung Felidae (`standard energetics of Felidae` von McNab (2000)) verglichen und auf Grundlage der Erkenntnisse der hier vorliegenden Arbeit neu diskutiert. Obwohl die ermittelten Stoffwechselwerte dieser Studie in der Grössenordnung der allometrisch berechneten Erwartungswerte für die Ordnung Felidae, aufgestellt von McNab, liegen, werden Unterschiede der Stichproben, Versuchsaufbau und Rahmenbedingungen (Tiere aus Gefangenschaft und frei-lebende Tiere) in McNabs Studie kritisch diskutiert.

Das 6. Kapitel dieser Arbeit untersucht die Verhaltensanpassung (Territoriumsgrösse (home range (95% aller GPS-Positionspunkte) und core area (50% aller GPS-Positionspunkte), Überlappung der Territoriumsgrösse und Aktivitätsmuster an eine semi-aride Insel. 15 Individuen wurden mit GPS- Halsbändern bestückt und für eine Dauer von drei Wochen wieder freigelassen. Die gesammelten GPS-Daten wurden analysiert und home range, core area und Überlappung dieser Variablen berechnet. Die Ergebnisse zeigen einen sehr hohen Grad an home range- (49%) und core area- (54%) Überlappung bei verwilderten Hauskatzen. Die hier vorliegende Arbeit ist somit die erste Studie, in der sich auch eine grosse Überlappung der core area findet. Dieses Ergebnis ist vermutlich auf eine hohe Beuteabudanz und limitiertem geeigneten Lebensraum für Katzen, verbunden mit einem geschwächten Territoriumsverhalten auf der semi-ariden Insel zurückzuführen. Fremde Katzen könnten möglicherweise dadurch in der home range und core area geduldet werden.

Fazit

Das Ziel der hier vorliegenden Arbeit war es, die Physiologie der verwilderten Hauskatze zu untersuchen und als einen möglichen Erklärungsansatz ihrer dichten Besiedlung des australischen Kontinentes zu diskutieren. Obwohl keine physiologische Adaptation an die aride Klimazone gefunden wurde, zeigt die Physiologie der Katze Flexibilität in der Anpassungsfähigkeit an Jahreszeiten und auch an Gefangenschaft. Diese gefundene Flexibilität weist darauf hin, dass sich Katzen an noch extremere Bedingungen physiologisch anpassen könnten. Aridität alleine könnte zudem keine ausreichende Extremsituation für Katzen dargestellt haben. Als interessante Folgestudien könnten sich Untersuchungen des Stoffwechsels nach vielen Jahren Dürre erweisen. Diese könnten vermutlich eine Stoffwechselanpassung, wie einen reduzierten Stoffwechsel, aufzeigen. Diese Studie zeigt zudem anschaulich die Verhaltensflexibilität der Katze, mit stark überlappenden home range und core areas. Diese Verhaltensanpassung stellt einen massiven Vorteil in der Besiedlung der verschiedenen Klimazonen Australiens dar.

Das Resümee dieser Arbeit ist, dass die erfolgreiche Besiedlung Australiens durch die Hauskatze vermutlich als eine Kombination verschiedener Anpassungen auf physiologischer und ethologischer Ebene zu erklären ist.

Summary

Feral cats (*Felis catus*), introduced into Australia with European settlers in the 19th century, colonized the entire Australian continent in less than 100 years, including the Australian arid zone which covers more than 70% of the continent. Feral cats are responsible for the decline and extinction of a number of native species and the failure of a number of reintroduction attempts, especially in the arid zone.

Many ecological studies on feral cats have been conducted on home range size and movement patterns in different environments, abundance and diet, with the aim of gaining a better understanding about their successful invasion of the Australian continent. There are no physiological studies on the feral cat to date. However, there is evidence that there is a strong interrelation between physiology and abiotic factors such as climate. Thus, distribution, habitat, and dispersal of species can not fully be understood without background knowledge of physiology. This PhD aims to contribute to a better understanding of three physiological parameters: metabolism, body mass and body temperature patterns. These parameters may possibly identify physiological adaptation to different climate zones, seasonal conditions and island isolation. It was hypothesized that cats would adapt to different challenging conditions (e.g. arid zone) by decreasing their basal metabolic rate and body mass, comparable to desert-dwelling Australian mammals, and that this would be a key to their successful establishment across the Australian mainland. This study however, did not find evidence for a decrease in basal metabolic requirement of cats from the arid zone, compared to their temperate and tropical counterparts, nor to same sized Felidae. Nevertheless, a decrease of body mass of cats from the arid zone was found. This however was believed to be due to an extensive trapping and baiting regime at one of the arid study sites eliminating larger dominant cats with established territories first, leaving a reduced population with a much higher proportion of younger and smaller cats. The basal requirement of cats in summer was 25% lower than in winter, possibly due to seasonal changes of food availability (reptiles and insects are mostly inactive during the winter) and the onset of the breeding season. This potentially might increase home range size in winter to meet daily food requirements and to find breeding partners.

Feral cats from two tropical islands were significantly smaller, compared to their mainland counterparts and also compared to feral cats from a semi-arid island, off Western Australia. This finding is believed to be possibly due to inadequate levels of certain nutrients on the tropical islands, rather than to climate (e.g. Bergmann's rule) or isolation (e.g. Island rule). The basal requirements of island versus mainland cats did not differ significantly, even though tropic adapted cats had a slightly but not significant higher BMR, possibly due to a high parasite infestation of cats.

Daily rhythm of body temperature (T_b) and activity (distance travelled) of free-ranging feral cats were recorded, via implanted body temperature loggers and Global Positioning System (GPS) technology (GPS- radio collars). The relationship between the activity (distance travelled) and T_b rhythms showed that the daily T_b rhythm is most strongly influenced by time of day, generated by an endogenous oscillator and that activity effects but does not determine the rhythm of T_b. No full synchronisation of both rhythms was detected, with T_b not being a by-product of the activity rhythm, which agrees with all previous studies on the relationship between these two rhythms.

To date, 90% of all physiological data available in the literature are derived from captive animals. This study however found an apparent change in physiological parameters with time in captivity,

with a 36% decrease in BMR of cats kept in captivity over a period of one year in comparison to freshly captures individulas. Furthermore, a change in circadian rhythmicity occurred, with a shift of activity patterns from nocturnal (free-ranging feral cats) to a diurnal tendency with a shift toward a decrease in amplitude of captive individuals. This clearly shows that captivity affects BMR and T_b variation in feral cats and therefore previously derived data from captive cats can not directly be applied to free-ranging populations. The latest study on the standard energetics of Felidae by McNab (2000) was used to demonstrate, how important 'good data' is for physiological comparisons. Even though, all four cat groups of this PhD fall within the 95% prediction limits for an additional datum from the relationship for the other Felidae species, the comparison highlights the inconsistence in McNab's data, combining data of captive (n=10 species) and wild animals (n=1 species) with eight out of 11 data points derived from a sample size of three or less.

The last chapter of this study moves from possible physiological adaptations of feral cats (Chapter 1-5) to flexibility in behavioural traits which potentially explain better how cats successfully colonised the Australian continent. Home range size, overlap and activity patterns of feral cats from a semi-arid island off Western Australia's coast were analysed and compared with other Australian feral cat populations, with very diverse results. This study is the first to show a core area overlap of more than 50%, possibly due to prey abundance and lack of suitable cat habitat, possibly resulting in a reduced territorial behaviour.

Introduction

Study background

The introduction of exotic animal species into naïve ecosystems has resulted in dramatic impacts on biodiversity in many places around the world. Understanding the biology, including physiology and ecology, of introduced species is crucial in developing practical strategies and methods of eradication or control. This is the challenge facing wildlife management agencies in Australia where the unique biodiversity is under threat from introduced animals. One species in particular, the cat (*Felis catus*), is threatening the survival of many unique mammals species on the Australian continent.

History of the cat

The domestic cat (*Felis catus*) is believed to be derived from the African or Arabian wildcat *Felis sylvestris lybica* (Randi and Ragni 1991; Bradshaw 1992; Serpell 2000). Domestication of the cat began about 8000 BC in Egypt in the eastern Mediterranean and continued until 4000 BC in the Middle East (Dickman 1996). Sculptures and paintings of cats from the 18th Dynasty confirm that cats were closely associated with humans and fully domesticated by 3600 BC. Slowly, domestic cats spread from Egypt all over Europe in the last 2000 years in close vicinity to human settlements. Today, domestic cats are distributed throughout the world wherever humans have colonized. They also occur on most of the world’s island groups. Many cat introductions took place deliberately in attempts to control rodent or rabbit populations (Flux 1993) in the 19th and early 20th century (Nogales *et al*. 2004).

Definitions

Although the focus of this thesis is on feral cats, it is difficult to distinguish between stray and feral cats in remote settlements, like mining operations or islands, where cats might be living on rubbish disposal sites and obtaining food from humans, but otherwise display behavioural traits of feral animals. The following definitions by Moodie (1995) have been adopted in this thesis.

- <u>Domestic cats</u> live in close connection with a household where all needs are intentionally provided by humans.
- <u>Stray cats</u> partly relying on humans for obtaining food and shelter.
- <u>Feral cats</u> are free-ranging cats which have minimal or no reliance on humans, and which survive and reproduce in self-perpetuating populations.

Australian fauna and European settlement

Australia is home to all three subclasses of mammals (monotremes, marsupials and placentals), including two species of monotreme (Prototheria), 159 species of marsupials (Metatheria) and 218 species of placental mammals or eutharians (Augee 1995). This unique faunal assemblage reflects a long period of isolation from other land masses with about 80% of Australia’s fauna being endemic to the continent (Strahan 1995). Since settlement by Europeans disrupted the isolation over 200 years ago, 22 of the original 306 terrestrial mammal species are now extinct (McKenzie and Burbidge 2002). Ten species, once widespread on the Australian continent, are confined to offshore islands and 43 species are threatened with extinction (McKenzie *et al.* 2007). Factors responsible for this drastic decline of the fauna include habitat changes from land clearing, altered fire regimes, and grazing by domestic stock, and the establishment of exotic plants and animals (Morton and Baynes 1985; Burbidge and McKenzie 1989; Dickman *et al.* 1993; Lee 1995; Lunney 2001; Johnson *et al.* 2002; Fisher *et al.* 2003).

A total of 17 exotic vertebrate species have been introduced into the country, including domestic animals that became feral as well as wild game animals, and are now widespread across the continent. Of these, two exotic predators – the European red fox (*Vulpes vulpes)* and feral cat (*Felis catus*) (Plate 1) – have become a major threat to Australia's wildlife (Wheeler and Priddel 2009).

The fox was successfully released in the 1870's (Rolls 1969) and today, has spread across the continent to all areas except parts of arid and tropical Australia. It has been largely responsible for the regional decline of medium-sized mammals (450-5000 g), birds and chelid tortoises (Friend 1990; Morris *et al.* 1995; Bailey 1996; Dickman 1996, Kinnear *et al.* 1998; Glen *et al.* 2009) and also for the failure of many wildlife translocation attempts (Short *et al.* 1992). Foxes are efficient opportunistic hunters as well as scavengers, and readily locate baits using their keen sense of smell. Effective methods for controlling foxes have been developed in Western Australia using dried meat baits or manufactured sausage baits injected with the toxin sodium monofluoroacetate or '1080' (Armstrong 2004). Baits are dispersed at a density of five baits per square kilometre from four to twelve times per year. Recovery of populations of native mammal species following the implementation of this baiting regime has been demonstrated at a number of locations in Australia (Kinnear *et al*. 2002, Friend 1990, Orell 2004).

Plate 1. European red fox (*Vulpes vulpes*) (Photo by S. Himer) Feral cat (*Felis catus*) (Photo by D. Algar)

Cats in Australia

The date of arrival of cats (*Felis catus*) in Australia is not known for certain, but it is generally accepted that the majority of cats were introduced during 1824-1886 by early European settlers because of their value in protecting domestic food from rodents (Dickman 1996; Abbott 2002). Cats may have been unable to become feral until the native predators (dingo, *Canis lupus*, tiger quoll, *Dasyurus maculatus* and wedge tailed eagle, *Aquila audax*) were suppressed around the settlements (Abbott 2002). During this period, it took approximately 10-20 years for cats to become feral, after which their population slowly spread outwards (Figure 1). With pastoralism, cats spread rapidly over the remaining desert area (Davison *et al.* 1987; Heathcote 1987). Furthermore, cats gained importance as predators once the rabbit (*Oryctolagus cuniculus*) plague began in the 1880's: it was illegal to kill feral cats in Western Australia between 1918-1921. Large numbers of cats were also deliberately released in arid and semi-arid regions in the 1880's as part of rabbit control programs (Rolls 1969). The introduced rabbit is also believed to have promoted the rapid colonisation of cats by providing a food source and also shelter in form of burrows (Morton 1990). Murray (1904) stated that '*generally more domestic cats than rabbits were seen, and these animals are now distributed right through the continent, and are almost as universal as the dingo*'. Today, feral cats are abundant across the entire continent, with cat density varying from 0.03 cats /km^2 in the Gibson Desert, Western Australia (Burrows and Christensen 1994) to 57 cats /km^2 on Great Dog Island in Tasmania (Hayde 1992). The density of cats changes seasonally and locally, most likely dependent on prey availability, favourable habitats and rainfall events.

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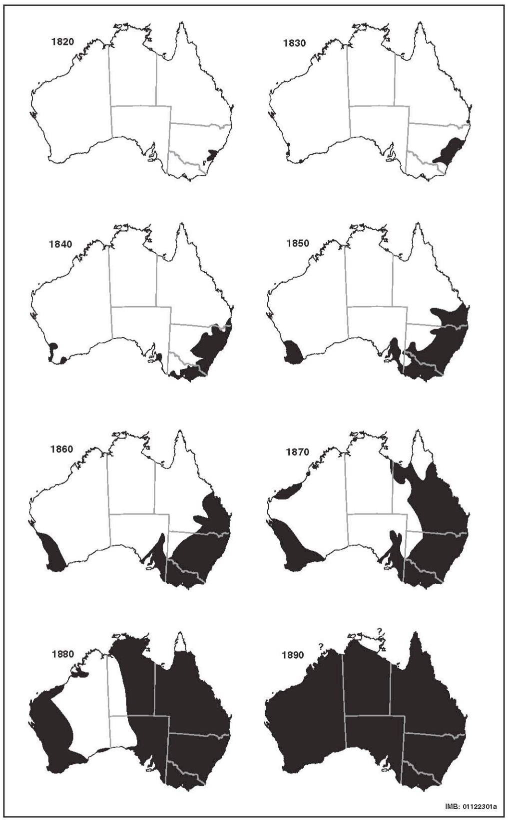

Fig. 3. Conceptual model of the colonisation of mainland Australia by the cat.

Figure 1. Conceptual model of the colonisation of mainland Australia by the cat (Abbott 2002).

Feral cats and the threat to native fauna

Feral cats are considered a major threat to Australian fauna by competing with native predators (Caughley 1980; Glen and Dickman 2005) and being hosts of diseases and parasites (Jones 1989; Dickman 1996; Yamaguchi *et al.* 1996; Turni and Smales 2001; Adams *et al.* 2008). However, the most destructive threat posed by the feral cat is through direct predation on native wildlife. A number of dietary studies demonstrate that feral cats are highly adaptable and opportunistic predators, capable of exploiting a wide range of prey species (Jones and Coman 1981; Dickman 1996; Paltridge *et al.* 1997; Risbey *et al.* 1999; Koch *et al.* submitted). The diet of feral cats includes mammals, reptiles, birds and invertebrates, depending on the availability and abundances of these prey species. This supports the belief that cats are responsible for the decline and extinction of a variety of native species (Veitch 1985; Burbidge and McKenzie 1989; Dickman 1996; Smith and Quin 1996; Risbey *et al.* 2000; Algar *et al.* 2002; Nogales *et al.* 2004; McKenzie *et al.* 2007; Glen *et al.* 2009). However, to determine whether the cat is exclusively responsible for early decline and extinctions of native animals on the mainland is difficult, due to the co–colonization by the rabbit and fox and changes in land use, overgrazing, soil compression and erosion. Nevertheless, there is extensive evidence that the introduction of domestic cats to both offshore and oceanic islands around the world had deleterious impacts on endemic land vertebrates and breeding bird populations (van Aarde 1980; Moors and Atkinson 1984; King 1985; Veitch 1985; Bloomer and Bester 1992; Bester *et al.* 2002; Keitt *et al.* 2002; Pontier *et al.* 2002; Blackburn *et al.* 2004; Martinez-Gomez and Jacobsen 2004; Nogales *et al.* 2004). Furthermore, feral cat predation has contributed to the failure of reintroduction attempts for a number of fauna reintroduction projects mainly in the arid zone (Short *et al.* 1992; Gibson *et al.* 1994; Christensen and Burrows 1995; Burbidge and Manly 2002).

Control methods for feral cats

Control of feral cats is recognized as an important conservation issue in Australia today and as a result, a national 'Threat Abatement Plan for Predation by Feral Cats' was developed (Anon, Environment Australia 1999). Management of introduced predators is now generally viewed as a critical component of successful reintroduction, recovery or maintenance of small to medium-sized native fauna populations (Christensen and Burrows 1995; Fischer and Lindenmayer 2000). Due to the significant impact of feral cats on native fauna decline, a number of methods have been tried to control/eradicate feral cats from strategic mainland locations as well as offshore islands (Algar and Burrows 2004). It has been shown that feral cats can successfully be controlled (Algar and Burrows 2004; Hilmer *et al.* 2009) and eradicated from offshore islands, with adequate baiting and trapping effort (Bloomer and Bester 1992; Algar *et al.* 2002; Bester *et al.* 2002; Algar *et al*. in press). However, on the mainland, it is more difficult to provide effective feral cat control over time because of reinvasion without extensive, ongoing time consuming and costly commitment.

To sustain a low number of feral cats in an area to release predation pressure on native animals and potential reintroduction of native fauna, an ongoing control strategy is required. Control of feral cats by trapping is generally expensive, labour-intensive and requiring continual application to be effective even over small areas. Trapping programs are usually only warranted to remove animals that have survived a baiting program where eradication is required or for research purposes. The most effective trapping method for feral cats uses padded leg hold traps, combined with lures e.g. 'Pongo' (blended faeces and urine), FAP (Felid Attracting Phonic) or food (Algar *et al*. 1999). These traps are usually set in 500-1000 m intervals along existing road systems or where cat tracks are detected. Traps must be visited after sunrise every morning, to avoid emotional and thermal stress for the animal.

Baiting is recognised as the most effective method of controlling feral cats (Short *et al*. 1997; van der Lee 1997; Anon. 1999; Algar and Burbidge 2000; Algar *et al*. 2002; Algar and Burrows 2004). A feral cat bait (*Eradicat*®) has been developed that contains the toxin `1080' (sodium monofluoroacetate) which is injected into the baits at a dose of 4.5 mg per bait (Algar and Burrows 2004). This bait has been used successfully in controlling feral cats at a number of mainland and island sites (D. Algar pers. comm.).

While foxes are scavengers and readily find baits and consume them, cats prefer live prey and hunt primarily by sight and hearing and therefore need further enticements to find and consume baits. To significantly increase the likelihood of cats taking baits, baiting campaigns are conducted during the late autumn/early winter when the abundance and activity of all prey types, in particular predator-vulnerable young mammals and reptiles, is at its lowest. Bait degradation due to rainfall, ants and hot, dry weather, is also significantly reduced (Algar and Burrows 2004). To further enhance the uptake by cats, baits are deployed from an aircraft at a density of 50 baits per square kilometre, a much higher density than required for foxes.

Physiology, ecology and environmental adaptation

Cat baiting programs are vulnerable in that climatic events or conditions could lead to extended periods of high prey abundance and therefore low bait uptake and ineffective control. Understanding the cat's physiology and ecology in terms of its environmental adaptations might point to vulnerabilities that could be exploited, leading to further refinements in the strategies and methods to control cats. The following parameters were targeted for investigation in this thesis to improve the understanding of the feral cat's adaptation to Australia's diverse environments.

Metabolism

Energy is the common currency of life, as it fuels biological processes at every level of organization. The metabolic rate is the rate at which an animal oxidizes substrates to produce energy.

Measurements of O_2 consumption or CO_2 production provide information on the amount of energy necessary for these processes, referred to metabolic rate (MR).

Metabolic rate (MR) can be measured by direct calorimetry, where metabolic heat production will be measured, or by indirect calorimetry, measurements of O_2 and CO_2. Another method of estimating MR is to determine the difference between energy ingested and energy excreted as urine and faces (Withers 1992).

Metabolic rate is influenced by several factors, like the body size, photoperiod, availability of food, digestion and food processing, body and air temperature and level of activity. The MR ranges from minimal value, when the animal is resting and fasted at thermoneutrality (basal metabolic rate), to the maximum metabolic rate, measured during intensive physical exercise, locomotion at high speeds, or for endotherms, during extreme cold stress. Furthermore, it is possible to evaluate the daily metabolic rate of animals under natural conditions, a parameter termed field metabolic rate. For estimating this parameter, the 'doubly labelled water method' can be used (e.g. Nagy 1987, 2005).

Body size

Body size is the most important factor influencing the metabolism in animals (West *et al.* 2003; Nagy 2005; White and Seymour 2005; McNab 2009). The interrelation between body mass and biological parameter is described by a power equation:

$$Y = \mathbf{a} \, \text{Mass}^{\mathbf{b}}$$

where **a** is the intercept and **b** is the mass exponent. This allometric relationship between metabolic rate and body mass is one of the most frequently investigated relationships (Withers 1992; White and Seymour 2005; McNab 2009). In particular, the understanding of the empirical scaling of BMR in mammals and its functional basis was investigated in many studies (Rubner 1883;

Kleiber 1932, 1961; Benedict 1938; Brody 1945; White and Seymour 2003).

Body size is known to be influenced by a variety of physiological, ecological and evolutionary characteristics (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Bonner 1988). Well-known rules discuss body size as evolutionary adaptation to climate (Bergmann's rule, Bergmann 1847) and island isolation (Island rule, van Valen 1973). The Bergmann's rule states that warm-blooded vertebrates from cooler climates tend to be larger than congeners from warmer climates (Bergmann 1847). Heat production in homeotherms is related to volume while heat loss is related to surface area. An increase in body size translates into a larger increase in volume than in surface area, and therefore, larger animals tend to produce more heat and will loose less heat. That is, large animals expend less energy for thermoregulation because of their surface to volume ratio, which is an advantage in cooler climates. Van Valen (1973) introduced the 'island rule', according to which small island mammals grow larger whereas large mammals tend to dwarfism. A reduction in body mass is accompanied by a reduced metabolic rate (Nagy 1987; McNab 1988) and therefore reduced individual resource requirements (McNab 2002) that may allow a larger and more sustainable population to survive in a limited geographical area.

Circadian physiology

Circadian physiology is a ubiquitous property of the physiology and behaviour of all known organisms (Turek and Van Reeth 1996). It is generated and maintained by endogenous clocks and triggered by external geophysical cycles. Rhythmicity persists under constant environmental conditions, displaying strong homeostatic properties, e.g. period length depends on light intensity but is temperature compensated. Under natural conditions, most animals have a pronounced daily cycle in body temperature and activity, which repeats itself approximately every 24 hours. Nocturnal animals are active during the night, whereas diurnal animals are sleeping during the night and are active during the day. Crepuscular animals are active during dusk and dawn. Important parameters of the body temperature rhythm are the mean level, amplitude and robustness (Figure 2, Refinetti 2006). The mean level of a time series, measures the central tendency of the data set. The amplitude refers to the full range of the parameter, in this case body temperature within a cycle. The robustness of a cycle is independent of amplitude and refers to the strength or regularity of the rhythm.

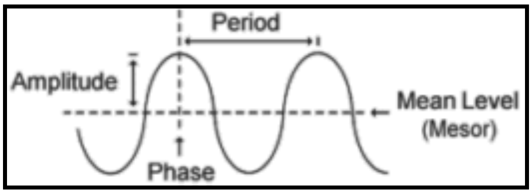

Figure 2. Rhythmic parameters characterized by mean level, amplitude, period and phase (from Refinetti 2006).

Home Range

A basic requirement when studying animals is an understanding of the relationship between the animal and its environment. Home range is a concept that describes the spatial context of an animal’s behaviour. It was formally defined by Burt (1943): “… that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.” The core area (50% of locations) may indicate higher concentrations of important resources, and are thus more important in understanding an animal’s life requisites (Powell 2000). The spatial context of animal behaviour is important not only in the management of threatened species but also in the management of threats (e.g. feral cats).

In the last 30 years, radio telemetry has been used to study animal locations and movement (Moen *et al*. 1996). In recent years, the combined deployment of Global Positioning System (GPS) technology and radio telemetry has become an important wildlife research technique (Rempel *et al.* 1995; D'Eon and Delparte 2005). Global Positioning System units calculate positions with information received from a set of 24 satellites orbiting the earth (Hurn 1989). The main advantage of GPS radio-telemetry over more traditional methods, such as VHF radio-telemetry, is the accumulation of large numbers of locations per radio-collar/animal through automated tracking. The increased number of locations per animal results in higher accuracy of individual home range and habitat use parameter estimates (Otis and White 1999; Girard *et al.* 2002).

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Aim of the thesis

While there is information about ecological and dietary traits of feral cats available in the literature, there is a paucity of physiological data which may be of significance in understanding the adaption of feral cats to Australia’s versatile environments. The study presented in this thesis aimed to contribute to a better understanding of three physiological parameters – basal metabolic rate (BMR), body mass (M_b) and body temperature (T_b) patterns – with regard to adaptation to different climate zones, seasonal conditions and island isolation. In addition, the effect of captivity on physiological patterns was investigated and quantified. In order to investigate behavioural adaptation of feral cats, home range size and movement pattern of feral cats on an island environment were studied.

The following chapters have been divided into three parts. The first three chapters investigate seasonal, climatic and island effects on metabolism and body mass of free-ranging feral cats, as well as the quantitative relationship between T_b and activity. Chapters 4 and 5 discuss the change in energy requirement and circadian rhythmicity of feral cats kept in captivity for extended periods and compare the data collected in this study with the latest study on the standard energetics of Felidae by McNab (2000). The sixth chapter departs from the field of physiology and investigates behavioural adaptation of a feral cat population in an island habitat.

As a whole, my thesis investigates a number of physiological and behavioural aspects of feral cats by examining both free-ranging and captive individuals, giving new information to provide a more comprehensive picture of the eco-physiology of feral cats in Australia.

Seasonal and climatic variations in basal metabolic rate of feral cats in Australia

Abstract

The influence of climate and season on the basal metabolic rate (BMR) of feral cats from Australia's arid and temperate zones was investigated. Little is known about physiological mechanisms that contribute to their ability to colonize a broad range of habitats. This study tested the hypothesis that physiology is closely correlated with ecological factors, resulting in cats from the arid zone having reduced BMR compared to their temperate counterparts. It further investigated the question if season influences the BMR of cats. Recently captured cats were used in this study to avoid the `captivity effect`, that has been shown to influence the BMR of feral cats (Chapter 4). Cats from the arid zone did not show a reduced BMR compared to cats from temperate regions (28119± 6005 Jh^{-1} *cf* 27835± 9929 Jh^{-1}), however BMR was lower in summer (24365 ± 5649 Jh^{-1}) than in winter (32620 ± 9061 Jh^{-1}; $P = 0.049$). This study indicated that the cat's basal requirement is not influenced by climate but by season, possibly due to different prey availability and changing activity patterns.

The key to the successful colonization of the Australian continent by cats is likely to be related to behavioural traits, including nocturnal activity and opportunistic hunting as well as the physiological ability of being independent of free water.

Introduction

Cats (*Felis catus*) were introduced into Australia in the 19th century by European settlers (Abbott 2002); by 1890 they inhabited nearly every region of the continent, including the arid zone covering more than 70% of the continent. Ecological studies of home range and habitat use by feral cats in different parts of Australia are diverse (Jones and Coman 1982b; Edwards *et al*. 2002; Molsher *et al*. 2005; Paltridge 2005), however little is known about the cat's physiological ability to adapt to Australia's variety of environments. It is thought that the domestic cat is derived from populations of African wildcats (*Felis silvestris libyca*) (Serpell 2000), well adapted to hot and arid conditions and even known to be independent of free water (Johnson 1991; Strahan 1995). Despite its abundance both as a domestic and a feral animal, few data were previously available regarding the cat's physiology. Data on the metabolic rates of laboratory animals date back to the early 1930s (Canon *et al.* 1929; Ring *et al.* 1931), however basal rates have not been measured (e.g. Adams 1963; Hensel and Banet 1982; Edstadtler-Pietsch 2003; Wichert *et al*. 2007). The metabolic physiology of feral cats has not been studied (Heusner 1982; Withers 1992; Lovegrove 2000; McNab 2000).

Many factors have been suggested to influence the level of energy requirements. Body mass (M_b) is generally acknowledged to be the most important factor setting the level of basal rate in mammals (Kleiber 1932, 1961; McNab 1980). Other factors have also been suggested as determinants of BMR, including body composition, body temperature, climate, phylogeny, diet, habitat, seasons and life history (Heldmaier and Steinlechner 1981; Hayssen and Lacy 1985; McNab 1986, 2000; Munoz-Garcia and Williams 2005; Li and Wang 2005; Careau *et al.* 2007; Smit and McKechnie 2009).

In this study, we investigated the potential difference in BMR of arid adapted cats in comparison to cats from the temperate zone. The desert climate offers a great physiological challenge to mammals; ambient temperatures can exceed 50°C accompanied by lack of drinking water, intense solar radiation and desiccating wind. Survival depends on an ability to adapt to these extreme conditions. A depression of BMR in arid-adapted mammals has been observed in several studies (McNab and Morrison 1963; Noll-Banholzer 1979; Lovegrove 2000; Careau *et al.* 2007), whereas other studies failed to find proof of a lower energy requirement (Afik and Pinshow 1993; Williams *et al.* 2002; Williams 2004).

This study aims to answer the following questions:

-Have arid adapted cats evolved physiological mechanisms to cope with challenging environmental conditions, e.g. reduced BMR and M_b?

-Does energy requirement of cats vary significantly between seasons?

Furthermore, this study focused on field measurements to avoid a potential `captivity effect` that might occur when using animals bred and reared in captivity, or wild-caught animals held in captivity for a long period of time (Nagy 1987; Speakman 1998; Nagy *et al.* 1999; Warnecke 2007; Schleucher *et al.* 2008). Standardized laboratory studies, although highly useful for comparisons amongst individuals and species, are of limited biological relevance because there is evidence that various parameters are significantly altered under captivity (Chapter 4).

Material and Methods

Study sites

The four study sites were located in Australia’s arid and temperate zones (Table 1).

Table 1. Study site summary, including number and sex of animals, measuring period and climate classification.

	Lorna Glen (LG) WA	**Mt Keith (Mt K) WA**	**French Isl. (FI) Vic.**	**Walpole (WP) WA**
No. of measured animals	7 (3♀, 4♂)	6 (2♀, 4♂)	6 (2♀,4♂)	4 (4♂)
Measurement period	summer	winter	summer	winter
Climate classification	arid	arid	temp.	temp.

The arid zone of Australia covers more than 70% of the Australian continent and is characterized by hot dry summers and cool winters. It is defined as an area receiving a mean rainfall of 250 mm or less. The arid study sites, Lorna Glen Station (26°13’S 121° 32.E’60) and Mt Keith (27°16’S 120°31’E) are located in the Gascoyne region of Western Australia. The climate is characterized by summer and winter rain, the annual precipitation is 200-250 mm (Figure 1). This region is located in the Ashburton Botanical District, which is dominated by mulga (*Acacia aneura*) often with snakewood (*A. xiphophylla*) and other *Acacia* spp. (Beard 1990).

Australia`s temperate (or Mediterranean) zone is characterized by dry, warm summers and wet, mild winters. Walpole (34° 57′ S 116° 43.60′ E) is located in the Karri Forest Subregion of Western Australia, which is dominated by tall Karri forest (*Eucalyptus diversicolor*) and forest of Jarrah- marri (*E. marginata; E. calophylla*) and paperbark (*Melaleuca*). The climate is described as moderate Mediterranean. Winter precipitation ranges from 650-1500 mm per annum with a short dry season of 3-4 months. French Island (38° 21′ S 145° 22′ E) is situated in the Gippsland Plain of Victoria. The mean annual rainfall varies from about 550-1200 mm, with the wettest months usually being from May-October (Figure 1). The vegetation ranges from mangroves and saltmarsh through to heaths and open woodlands.

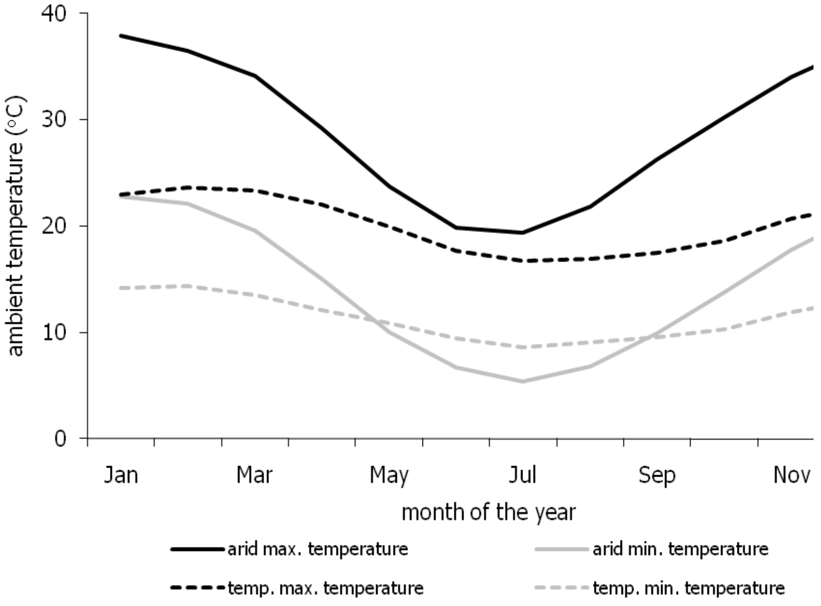

Figure 1. Minimum and maximum ambient temperatures of arid (Lorna Glen, Mt Keith) and temperate (French Island, Walpole) study site. Data obtained from the Bureau of Meteorology (www.bom.gov.au).

Trapping procedure

In total, 23 (7♀, 16♂) cats were caught across the different study sites in summer and winter (Table 1). Cats were trapped using padded leg-hold traps (Victor 'Soft Catch'® traps No. 3; Woodstream Corp., Lititz, Pa.; U.S.A.) with a combined lure system of a blended mixture of cat faeces and urine ('Pongo') and a Felid Attracting Phonic (FAP) that produces a sound of a cat call (Algar *et al.* 2002). Traps were located at 500 m intervals along existing roads/tracks at each of the sites. The trapping success, based on the trap nights and number of animals caught, was between 5-10%. All cats used in this study were sexually mature, based on the minimum weight for sexual maturity for cats: 2400 g: females, 2600 g: males (Jones and Coman 1982a; Jones 1989).

Experimental set up

Metabolic rates were measured via indirect calorimetry by using a one-channel oxygen analyser (Servomex 572B, measuring range 0 – 100 Vol. %, accuracy ± 0.1%), which was calibrated against pure oxygen and nitrogen (see review by Withers 1991). Re-calibration was conducted at the beginning and end of each experiment against ambient air. Instrument output was read by a voltmeter (Voltcraft VC 840), which transferred the data through an RS 232 interface to a PC for data collection. Gas volumes were corrected for air pressure fluctuations and reduced to STPD (standard temperature, pressure and dry conditions). Cats were placed in a plastic metabolic chamber with clear plexiglass front (35x 35x 40 cm) with a second exit at the rear of the chamber to enable removal of the cat without direct handling.

Pre-dried room air (silica gel with non-toxic humidity indicator) was passed through the chamber using an adjustable membrane pump (Type: WISA) at a rate of 550 L h^{-1}. Outgoing chamber air was passed through a drying column of Silica gel and via bypass. Eight L h^{-1} were sampled by a second pump (WISA) and passed through a set of three drying columns (Silica gel/ Drierite ($CaSO_4$)). Flow rates were constantly monitored via a flow meter (Rota Yokogawa, L 742 11484, 40-630 L h^{-1}; Rota Yokogawa, 860806.4403; 0.16-10 L h^{-1}). Humidity was constantly monitored by a humidity probe (Hygrotest 80, Testoterm GmbH & Co., Lenzkirch) in an airtight container in the air stream, and then passed through a fine filter before entering the analyser. The metabolic chamber was placed in a controlled temperature cabinet (50x 55x 100 cm, accuracy ± 1°C) and the first hour of measurement was discarded from data analysis.

One measurement per cat at thermal neutral zone (TNZ, 28-30 °C, Hilmer 2005; Schleucher *et al.* 2008) was conducted on-site, on the same day of capture (16:00-7:30h). The cats were kept without food and water in a dark, quiet room for several hours before the experiment to allow relaxation. All cats adjusted quickly to the experimental protocol, and did not exhibit visible indications of stress. Cats were humanely destroyed after the experiment.

Statistical Analysis

Values are presented as means ± standard derivation with sample size (n), calculated from each individual cat. The influence of season, climate and sex on body mass (M_b) and on basal metabolic rate (BMR) was investigated. A general linear model (analysis of covariance; SPSS) was used to investigate effects of the above variables on log transformed M_b and BMR data. M_b was used as a covariant when analysing the effect of variables on BMR. The effect of body mass on BMR was determined by linear regression and full factorial ANOVA, using StatistiXL (version 1.8).

Results

Body mass

Differences in sex, locality and season on body mass (M_b) were investigated. M_b was significantly different between sexes, with a higher body mass for male cats (3988 ± 690 g; n= 16) than for female cats (2771 ± 381 g, n= 7; $P > 0.0001$). Also, cats from the temperate zone had a higher M_b (4020 ± 794 g, n= 10) than cats from the arid zone (3308 ± 745 g, n= 13; $P = 0.028$). No significant difference in M_b could be detected between localities

(P = 0.1029). No significant 2-way interaction could be determined (Table 2). Pooled male and female M_b data provided a mean value for feral cats of 3617 ± 832 g (n= 23).

Table 2. Results of analysis of covariance of body mass. Log-transformed data used in analysis. The model was significant (R^2 = 0.744, F= 9.87, *d.f* = 5, $P < 0.0001$).

Source	*df*	Mean Square	F	Sig.
Season	1	0.010	2.970	0.103
Sex	1	0.057	16.536	0.001
Locality	1	0.020	5.738	0.028
Season * Sex	1	0.008	2.280	0.149
Season * Locality	1	0.010	2.848	0.110

Basal metabolic rate

The potential influence of sex, locality and season on BMR was tested with M_b as a covariant. Body mass has a significant influence on BMR (P = 0.025, Table 3, Figure 2). The analysis showed that season does have a significant effect on BMR with a higher BMR in winter (32630 ± 9061 Jh^{-1}) than in summer (24365 ± 5649 Jh^{-1}; P = 0.049). Sex and locality, however, did not have a significant influence on BMR (Table 3). Because no significant difference in BMR between sexes was detected, pooled data of both sexes was used (Table 4). No significant 2-way interactions were found.

Table 3. Results of analysis of covariance of BMR. Log-transformed data used in analysis. The model was significant (R^2 = 0.561, F= 5.682, *d.f* = 6, P = 0.0025).

Source	*df*	Mean Square	F	Sig.
Season	1	0.031	4.532	0.049
Sex	1	0.000	0.065	0.802
Locality	1	0.006	0.869	0.365
Season * Sex	1	0.007	1.064	0.318
Season * Locality	1	0.001	0.180	0.677
M_b	1	0.042	6.084	0.025

Table 4. Mean Body mass (M_b), Basal metabolic rate (BMR in Jh^{-1}) ± SD and number of animals (n) from both climatic zone and season.

		M_b [g]	BMR [J h^{-1}]	n
Temperate cats	summer	4000 ± 1049	25860 ± 5252	6
	winter	4050 ± 238	31778 ± 5698	4
	mean temp.	4020 ± 794	28119 ± 6005	10
Arid cats	summer	2971 ± 647	23238 ± 6134	7
	winter	3700 ± 699	33198 ± 11285	6
	mean arid	3308 ± 745	27835 ± 9929	13

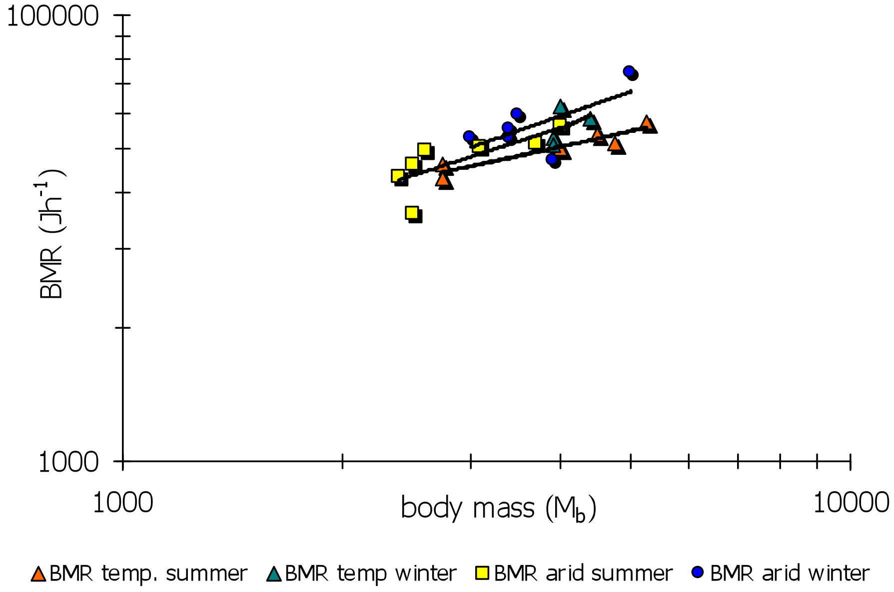

Figure 2. Relationship between basal metabolic rate (BMR) and body mass (M_b) of feral cats measured in this study with corresponding regression lines. (temp=temperate zone, arid=arid zone, summer/winter=data point collected in summer/winter) (Log scaled).

Regression equations for different study groups:

$BMR_{\text{temp. summer}}$: $74\ M^{0.7058}$ $R^2 = 0.8874$

$BMR_{\text{temp. winter}}$: $0.0076\ M^{1.56}$ $R^2 = 0.2507$

$BMR_{\text{arid summer}}$: $4.92\ M^{1.0563}$ $R^2 = 0.5582$

$BMR_{\text{arid winter}}$: $2.72\ M^{1.1423}$ $R^2 = 0.4346$

Discussion

The sex ratio of the study animals was uneven (16 ♂, 7 ♀) due to the low and unpredictable trapping success. However, our results supported a common finding that adult female cats are generally lighter than male cats (Read and Bowen 2001). Body mass did not change significantly between seasons but differed significantly between localities, with cats being heavier in the temperate zone. This finding supports other studies which describe a decrease in body size of desert mammals compared to their mesic counterparts (Geffen *et al.* 1992). It could be explained by the 'resource limitation hypothesis' i.e. body size has been reduced through evolution to lower the energy requirements of animals in response to limited food resources. However, in this study, it is questionable if the difference in M_b is the result of an evolutionary body size reduction as the difference between zones may be an artefact. The summer study site in the arid zone (Lorna Glen Station) has been subject to a long-term cat control program since 2003 (Algar, unpublished data). Consequently, large, mature cats rarely occur in this area anymore and are replaced by young adult cats dispersing into the site from adjacent non-baited areas, which might be reflected in the smaller body mass. Chapter 2 agrees with this argument, as failing to find an M_b difference of long term trapping data from temperate and arid adapted cats.

Body mass is acknowledged to be the primary influence of BMR in mammals (Kleiber 1932, 1961; McNab 1980), and this relationship was also shown to be significant in this study. Other factors, such as climate, have also been suggested as determinants of BMR. Many studies have investigated the relationship between climate and BMR with diverse results; some studies have shown a depression in BMR in mammals in arid environments (McNab and Morrison 1963; Noll-Banholzer 1979; Golightly and Ohmart 1983;

Lovegrove 2000, 2003), whereas other studies have found little adjustment (Afik and Pinshow 1993; Williams *et al.* 2002, 2004). In this study, no evidence was found that cats from the arid zone show a depression in BMR compared to their temperate counterparts. Nevertheless, a physiological adaptation (e.g. reduction in BMR) as a possible adaptation factor to challenging conditions can not be excluded. Animals used in this study were all in very good conditions, without any signs of hunger or starvation. It would be possible that starving individuals would decrease their basal requirement, shown in artic foxes (Fuglei and Øritsland 1999), which would not be limited to an arid environment, rather than to low prey availability. This however, was not possible to determine under field conditions, due to ethical reasons, limitations in holding capacity for cats in the field and possibly very high stress levels of starving cats, potentially influencing the measurements of basal values.

If it is not the depression of energy requirements, what other characteristics enable the cat to colonize the entire Australian continent, especially the hot and dry arid zone? The most striking advantage the cat has compared to the red fox *(Vulpes vulpes*), another of Australia’s introduced predators, is that cats are independent of free water (Strahan 1995). Hence, cats are present on the entire Australian continent whereas the red fox is absent in the dry northern arid zone of Australia presumably due to the lack of free water. Also, cats are mostly inactive during the day (Chapter 3, Chapter 6), using shelters in the form of rabbit warrens and tree hollows where the ambient temperature is stable (Edwards *et al.* 2001). Golightly and Ohmart (1983) made similar observations studying the kit fox (*Vulpes macrotis*), a ~2000 g desert canid. This species is found in the Great Basin Desert of North America and is also independent of free water. The kit fox has not evolved physiological mechanisms to cope with high ambient temperatures;

instead it reduces the time of activity to periods of low exogenous heat loads and therefore avoids extremely high temperatures. Cats also face other challenges in the arid zone, particularly the seasonal and yearly fluctuations of food resources or prey availability. Cats are highly adaptable and opportunistic hunters (Paltridge 2002) and the diet includes mammals, reptiles, birds and invertebrates, depending on the availability and abundances of these prey species. The seasonal availability of food might influence the energy requirement of the cat, leading to a lower basal metabolic rate in the summer than in the winter. Munoz-Garcia and Williams (2005) found that in Carnivora, BMR and home range size were significantly correlated and that diet was correlated with home range size. They concluded `*that species that eat meat have larger home ranges and higher BMR than species that eat vegetable matter*`. The cat is exclusively carnivorous, however, reduced prey availability in the winter, when reptiles, amphibians and invertebrates are less active, could also lead to extended home ranges and longer, extensive hunting periods with active phases also during the day. Mc Nab (1986) argues that vertebrate eating mammals have a higher BMR than mammals eating a mixed diet or an invertebrate diet. Paltridge *et al.* (1997), who examined the diet of feral cats in central Australia, found that invertebrates were part of the cat's diet all year round, but significantly more important in the summer. Bayly (1978) confirmed this finding with invertebrates comprising 14% of the cats diet in the summer (March), compared to just 0.5% in the winter (July). The results of these studies taken together suggest that the cat should have a larger home range and higher BMR in the winter than in the summer; certainly the BMR was found to be higher in winter in this study. Clearly, more work needs to be done on the actual food intake of cats to be able to demonstrate any correlation between diet and BMR. Other environmental conditions could also influence the energy requirement of mammals and may vary with changes in seasons, like photoperiod, rainfall and ambient temperature. The increase of BMR in winter is confirmed by others studies, mainly on small mammal species (Lynch 1973; Heldmaier and Steinlechner 1981; Merritt 1986, 2001; McDevitt and Speakman 1996; Li and Wang 2005). Animals in summer decrease their energy requirements to lower their metabolic heat production and therefore the body temperature. A higher BMR in winter is likely to reflect the greater need for oxygen-consuming thermogenesis at lower temperatures (Larcombe and Withers 2008). However, simple `cause-and–effect` relationships must be viewed with caution and this has been recognized in the literature (Cruz-Neto and Bozinovic 2004). Diet and energy saving mechanisms might be part of the answer, however at this point not enough information is available to link changes in BMR to one factor in particular.

Without doubt, the cat is one of Australia’s most successful fauna introductions. Their successful establishment, especially in the arid zone, is linked to behavioural traits such as nocturnal activity, flexibility in prey selection (allowing effective exploitation of available prey species) and the ability to survive without free water. No evidence of a decrease in basal requirements of feral cats in the arid zone was found in this study and it appears that such a physiological adaptation is not necessary for this species to survive in arid environments.

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Comparison of basal metabolic rate and body mass of Australian island versus mainland feral cats

Abstract

This study compares the relationship of body mass, M_b, (male cats only) and basal metabolic rate, BMR, between feral cat populations on the Australian mainland and a number of islands. These comparisons also include different climate zones, already addressed in Chapter 1 and further discussed here. M_b of tropical and temperature island cats had a significant lower M_b compared to cats from a semi-arid island and mainland cat population, whereas no difference in BMR was found between groups. The observed difference in M_b is discussed with reference to Van Valen's (1973) 'island rule' and Bergmann's Rule (Bergman 1847). No support for island or climatic adaptation of feral cats was detected and this study concludes that the reduced body mass of cats from tropical islands is possibly due to a high parasite infestation. Future studies on body mass comparison need to focus on even sample sizes and sites which have experienced previous cat control programs need to be excluded from evaluation to avoid a bias in the data.

Introduction

Feral cats (*Felis catus*) have become established in a range of climatic zones throughout the world wherever humans have colonized, and occur on most of the world's islands (Long 2003). Both climate and isolation on islands have been important influences on the evolutionary adaptations in a range of vertebrate species around the world (e.g. Blackburn and Hawkins 2004; Lomolino 2005) but no study has investigated potential influences on feral cat populations.

A series of bioclimatic rules have been proposed to explain the variation in body morphology e.g. Cope's rule, Allen's rule and Gloger's rule (Withers 1992; Damuth 1993). Islands have served as models of evolutionary and ecological phenomena ever since Darwin's observations and publications (Darwin and Wallace 1858). Among the most pronounced microevolutionary changes occurring on islands are body size changes, most apparent in mammals (McNab 1994; Clegg and Owens 2002; Meiri *et. al* 2004). Foster (1964) carried out the first systematic analysis of body size patterns of insular mammals. By surveying the literature, he found that island rodents usually tend to gigantism, whereas carnivores, lagomorphs, and artiodactyls are characterized by insular dwarfism. Following Foster (1964), Van Valen (1973) introduced the 'island rule', according to which small island mammals grow larger whereas large mammals tend to dwarfism. He noted in his study, that `*mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals*`. Several hypotheses have been raised to explain this phenomenon, including limited island resources, island size and inter - specific competition and predation (Case 1978; Heaney 1978). A reduction in body mass is accompanied by a reduced metabolic rate (Nagy 1987; Mc Nab 1988) and therefore reduced individual resource requirements (Mc Nab 2002) may allow a larger and more sustainable population to survive in a limited geographical area.

Bergmann’s rule states that warm-blooded vertebrates from cooler climates tend to be larger than congeners from warmer climates (Bergmann 1847). Heat production in homeotherms is related to volume while heat loss is related to surface area. An increase in body size translates into a larger increase in volume than in surface area, and therefore, larger animals tend to produce more heat and loose less heat. That is, large animals expend less energy for thermoregulation because of their surface to volume ratio, which is an advantage in cooler climates.

This study will evaluate potential evolutionary and ecological adaptations of feral cats to island and climatic conditions, by comparing body mass and energy requirement of island versus mainland cat populations as well as cats from three different climate zones, temperate, semi arid and tropics.

Material and Methods

Study areas

Table 1. Study site summary, including number and sex of animals (M_b comparison, only males) and climate classification (data obtained from: [1]Algar *et al.* 2003; [1]Hilmer *et al.* 2009, [2] M. Johnston, unpublished data, [3]Johnston *et al. 2009*, [4] DEC internal reports).

	Island				**Mainland**	
	Cocos Isl.	Christ-mas Isl.	Dirk Hartog Isl.	French Isl.	Lorna Glen	Bronzewing Jundee, Mt Keith
climate	tropic	tropic	semi arid	temp.	arid	arid
BMR (n)	4♀, 5♂	4♀, 4♂	/	2♀, 4♂	3♀, 4♂	/
M_b (n)	70 [1]	23 [2]	13 [3]	44 [2]	/	59 [4]

Island populations

<u>The Cocos (Keeling) Islands</u> (12^0 12'S, 96^0 54'E) are an external Australian territory, 2768 km northwest of Perth, Western Australia. The islands are two coral atolls only several metres above sea level which have developed on top of old volcanic seamounts. The inhabited southern atoll is 14 km long and 10 km across and comprises 26 islands (population size: 596 in 2007). The vegetation on the southern atoll is dominated by groves of coconut palms (*Cocos nucifera)*. The understorey is mostly coconut seedlings with some shrubs, grasses or other perennials or a dense mat of decaying palm fronds and coconuts. These woodlands are fringed on the lagoon shore by a shrub land of *Pemphis acidula* and on the

ocean shores by cabbage bush (*Scaevola taccada*) and clumps of octopus bush (*Argusia argentea*) (Williams 1994; Woodroffe & McLean 1994).

Christmas Island (10°25′S,105°40′E) is situated 900 km northeast of the Cocos (Keeling) Islands. The oceanic island is composed primarily of Tertiary limestone overlying volcanic andesite and basalt (Tidemann *et al*. 1994; Environment Australia 2002). The island is mostly covered in tropical rainforest. The climate of the Cocos (Keeling) and Christmas Islands are described as tropical, with high humidity (80-90%), little ambient temperature amplitude (22 °C minimum, 28 °C maximum) and with an average annual rainfall of 2150 mm.

Dirk Hartog Island (25°50′S 113°0.5′E) is located approximately 850 km north of Perth, Western Australia and covers an area of 620 km^2. Vegetation is generally sparse, low and open (for more information, see Chapter 6). The climate is semi-arid, receiving an average of approximately 224 mm of rainfall annually with most of the rain occurring historically during May-July with annual minimum and maximum temperatures of 12-32 °C (Bureau of Meteorology).

French Island is located in Western Port, Victoria (38°21′S 145°22′E) and covers approximately 17000 ha. French Island National Park (11100 ha) is the largest land use on the island and includes very dense melaleuca *(Melaleuca* sp.*)*, heathland vegetation, eucalypt (*Eucalyptus* sp.), woodland and coastal mudflats (Weir and Heislers 1998). The climate is described as temperate, with a mean annual rainfall of 780 mm and a annual temperature of 8 (minimum) and 24 °C (maximum) (Bureau of Meteorology).

Mainland populations

Lorna Glen (26°13′S 121° 32. E′60), Mt Keith Mine Site (27°16′S 120°31′E), Jundee Mine site (26° 21′ S 120° 38′ E) and Bronzewing

Mine site (24^0 60′S 120^0 58′E) are situated in the Austin Botanical District, Murchison Region and Wiluna Sub-region (Beard 1976). The vegetation units most common across the study area are tree and shrub steppe on sand plain, primarily Mallee (*Eucalyptus kingsmillii*) and Mulga (*Acacia aneura*) over hard spinifex (*Triodia basedowii*). The climate is classified as arid with a mean rainfall of less than 300 mm per annum and annual minimum and maximum temperatures ranging from 5-38 °C (Bureau of Meteorology).

Body mass comparison

For the comparison of Body mass (M_b) of island and mainland cat populations, data collected during trapping surveys from four island and three mainland populations were used (Table 1). M_b data from the mainland were taken from three closely situated remote study sites in the Western Australian inland (Jundee, Bronzewing and Mt Keith). These sites were chosen because of their remoteness and therefore minimal potential for contact with domestic animals. Data were collected over a period of several years during cat control programs by DEC staff.

The reproductive state of the female cats (e.g. pregnant, lactating) was rarely recorded during these surveys. As the reproductive state would significantly affect the body mass, a decision was made to discard the data from female cats from the body mass comparison. Only M_b data of sexually mature male cats were used (2600 g; Jones and Coman 1982; Jones 1989). No significant difference between the Cocos (Keeling) and Christmas Islands was detected (P = 0.94), and therefore the M_b data of these tropical island populations were combined.

Metabolic measurements

Animals

Cats were captured on Cocos (Keeling), Christmas and French Islands (Table 1). The trapping technique used on Cocos and Christmas Islands employed cage trapping around the settlement, a fish lure and leg hold trapping in the unpopulated areas in the National Park and remote jungle area (see Hilmer *et al.* 2009). Trapping on French Island included cage and leg hold trapping. It was not possible to carry out any metabolic measurements on Dirk Hartog Island, due to unreliable power supply, which is essential for the experiment.

Experimental set-up

Captured cats were held without food and water *ad lib.* in a dark, quiet room for several hours before the experiment to promote resting. Metabolic rates were measured via indirect calorimetry (Chapter 1). One measurement per cat at a T_a representing the thermoneutral zone or TNZ (28-30 °C) was conducted on-site at the day of capture (16:00-07:30 h). No temperature cabinet was necessary on Cocos (Keeling) and Christmas Islands, because the very stable ambient/room temperature was representative of TNZ (28 °C). All cats adjusted quickly to the experimental protocol, and exhibited no indications of stress. Cats were humanely destroyed after the experiment.

The BMR of the three island populations (Cocos (Keeling), Christmas and French Islands) were compared with BMR data of one Australian mainland population: Lorna Glen (n=7, see Chapter 1). This population was chosen, because mainland populations show an apparent seasonal difference in BMR (Chapter 1). Measurements on French Island were conducted in the summer and therefore, the mainland comparison used summer values as well. However, Christmas and Cocos (Keeling) Islands are located in the tropical climate zone, where seasons are characterized by dry and wet season rather than summer and winter and no significant T_a amplitude is present. Nevertheless, measurements on both islands were conducted in November, which was considered equivalent to summer on the Australian mainland. Chapter 1 showed that BMR of feral cats is independent of sex and therefore data of male and female cats were pooled.

Statistical Analysis

M_b and BMR values are presented as means ± standard derivation with sample size (n). An ANOVA was used to test for significant differences in BMR of three cat populations: island-temperate (FI), island-tropics (Cocos (Keeling) and Christmas Islands) and mainland-arid (Lorna Glen). An ANOVA was also used to test for significant differences in M_b of the following groups: island-semi arid (DHI), island-temperate (FI), island-tropics (Cocos (Keeling) and Christmas Islands), mainland-arid (Jundee, Bronzewing and Mt Keith). A turkey HSD (Honestly Significant Difference) test was used to determine differences between two populations. It was not possible to use an ANCOVA, with climate and island/mainland as co factors, due to missing BMR and body mass values of mainland tropics, mainland temperate cats and mainland semi-arid.

Results

Body mass

The tropical island male cats had a significant lower M_b (3490 ± 577 g, n= 87) compared to cats from the semi-arid island, (4530 ± 838 g, n= 13; *P* < 0.0001) and their mainland counterparts (4130 ± 744 g, n= 59; *P* < 0.0001). Cats from the temperate island had a significantly smaller body mass (3780 ± 104 g, n= 44) compared with cats from the semi-arid island (*P* < 0.001) as well as the mainland (*P* < 0.01). No significant difference was found between body masses of cats from the semi arid island and the mainland (*P* = 0.09) (Figure 1).

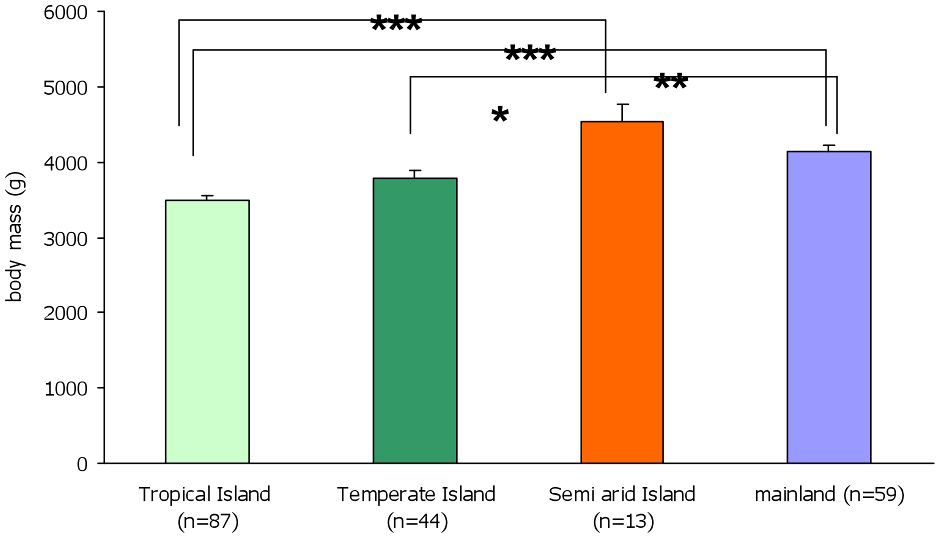

Figure 1. Body mass (g) (± SE) comparison of island and mainland male cats with significant differences (*= *P* <0.01) calculated with Turkey HSD test.

Basal metabolic rate

No significant difference was found between the BMRs of island cat populations (Cocos (Keeling) Islands: 32632 ± 9838 Jh^{-1}, n= 9; Christmas Island: 26506 ± 9129 Jh^{-1}, n= 8; French Island: 25682 ± 5252 Jh^{-1}, n= 6; $P = 0.237$)) nor between the island groups and the mainland cat population (Lorna Glen: 23238 ± 5649 Jh^{-1}, n= 7; $P= 0.23$) although there is a clear trend for the animals from colder (temperate , blue) or more variable (arid, red) climates to have lower rates than the populations from the tropical islands (Figure 2).

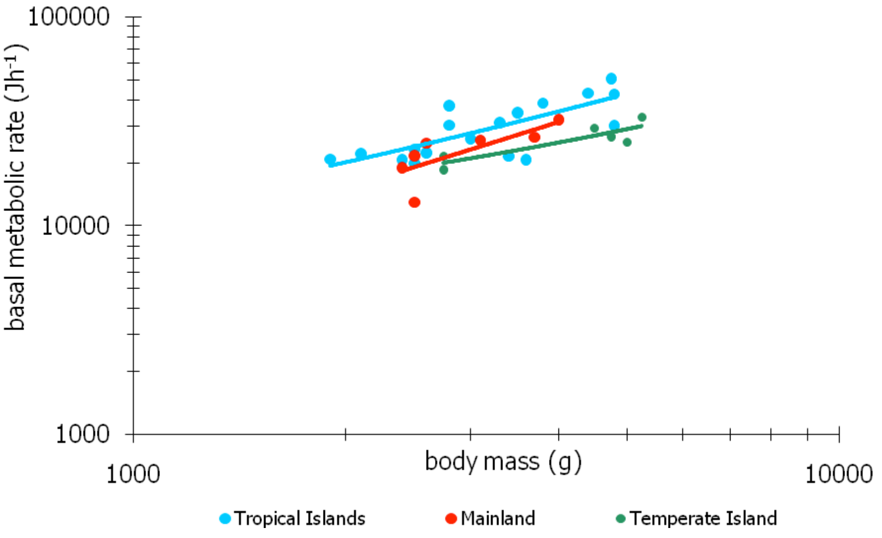

Figure 2. Relationship between basal metabolic rate (BMR) and body mass (M_b) of feral cats of tropical island (blue circle), temperate island (green circle) and mainland population (red circle) with corresponding regression lines (Log scaled).

Regression equations:

$BMR_{\text{tropical island}}$: 23.411 $M^{0.884}$ R^2: 0.595

$BMR_{\text{temperate island}}$: 153.2 $M^{0.6149}$ R^2: 0.769

BMR_{mainland} : 4.915 $M^{1.0563}$ R^2: 0.558

Discussion

This study was conducted after a field trip to two tropical islands, the Cocos (Keeling) Islands and Christmas Island, where an apparent smaller body size of the island cats raised the question: "was this apparent M_b decrease due to the island isolation or to the tropical conditions?" Consequently, body mass data of previous trapping exercises of four island and three mainland cat populations were used to quantify differences in M_b against the background of island isolation and climatic adaptation. No body size measurements were available for analysis, hence only a comparison of body mass was possible. Cats from the tropical and temperate islands showed a significantly smaller M_b compared to cats from the mainland, whereas M_b data of cats from the semi-arid island did not show a significant difference to the mainland counterparts. Studies on mammalian body size adaptations to different environments (e.g. deserts, fragmented land systems, islands) are diverse. This study selected two prominent rules, the 'Island rule' and Bergmann's rule, as potential explanations for the M_b differences between the study groups.

The 'Island rule' (Van Valen 1973) states that on islands, small mammals grow to larger size whereas large mammals tend to dwarfism. Many studies have since proposed mechanisms, like resource limitation, dispersal ability, and competitive release as explanations for this body size pattern (Grant 1965; Lawlor 1982; Lomolino 1985; 2005). Cats were introduced to all three island groups with early human settlers in the 19th century and this study investigates potential morphological adaptations shown by this species. Recent studies have shown that many organisms can in fact undergo adaptive genotypic and consequently phenotypic adaptation over just a few generations. Schmidt and Jensen (2003) found that over 175 years, mammals that live in fragmented land systems in Denmark, do change their body length significantly, possibly responding to increasing habitat fragmentation. However cats from the tropical and temperate islands have not been completely isolated; cats have been brought as pets to the island groups until recently. Therefore, an island effect could possibly be excluded as an explanation for the lower M_b of these island cats. Additionally, cats from the semi-arid island (Dirk Hartog Island) have been isolated for many generations and they fail to show a decrease in body mass. This finding is consistent with Meiri *et al.* (2004) who found little support for the island rule for carnivores, proposing that the body size is influenced by several selective forces, including life history and abiotic factors and that body size patterns are more complex than the 'island rule' predicts.

The Bergmann's rule states that within mammalian species, individuals tend to be larger in cooler environments in order to reduce their surface-volume ratio (Bergmann 1847, translated in James 1970). When applying the Bergmann's rule to the data from this study, it could be assumed that cats from the coldest study site, the temperate island, would show the highest body mass. This however is not the case, with temperate island cats being significantly smaller than cats from the semi-arid island and mainland populations. Furthermore, this supports the finding that the smaller M_b of arid cats found in Chapter 1 were due to a long-term trapping exercise, rather than a reduction in M_b to adapt to resource limitation, because it is not apparent in arid cats in this study. In addition, many studies have since criticized Bergmann's empirical generalization (Scholander 1955; Irving 1972; Geist 1987). Alternative hypotheses to latitude and temperature as factors for the Bergmann's rule have been offered (McNab 1971; Ashton *et al.* 2000), which include primary productivity, prey frequency and food quality and abundance, consistent with mechanisms explaining the island rule (see above). Feral cats are generally known as generalists and opportunistic hunters, preying on a wide range of prey species. Several studies on the diet of feral cats on islands report a dietary dependency on introduced mammals when abundant (Coman and Brunner 1972; Bloomer and Bester 1990; Fitzgerald *et al*. 1991; Nogales *et al*. 1992; Barratt 1997). A study on Macquarie Island (Jones 1977) showed that rabbits contribute more than 80% of the cat's diet. A relationship between mass and food quality and prey abundance is also obvious in this study, even though food quality and prey availability has not been specifically measured. While conducting the cat-trapping exercise on Dirk Hartog Island, prey abundance, especially rodents, was observed to be very high across the island (Chapter 6). In contrast, a comprehensive diet study on cats on the Cocos (Keeling) Islands indicated that cats preyed on grasshoppers and rats (*Rattus sp.)* but the majority of stomachs contained household scraps (Algar *et al.* 2003). This shows the limited availability of nutritious prey species and a likelihood of a co-dependency to humans. In populations of wild mammals with food-limitation, ecological factors can affect growth rates of juveniles before or immediately following birth, which can have pronounced consequences for their growth, survival and breeding success (Lummaa and Clutton-Brock 2002). Insular white-tailed deer (*Odocoileus virginianus*) decreased their body size up to 50% when resources were limited, however they increased in size when well fed (Sinclair and Parkes 2008). Therefore, phenotypic plasticity could be the reason for the smaller M_b of tropical cats, due to lack of nutrients, which might be reversible when cats would have access to unlimited, nutritionally valuable food. Also, a high parasite infestation has been found in cats of Christmas Island, (e.g. *Toxoplasma gondii* (24 out of 25 samples), *Toxocara cati* (15 out of 28 samples), *Strongyloides sp*. (13 out of 28 samples), Adams *et al.*

2008), which could effect the early development of kittens, resulting in a lower body mass.

A decrease of energy expenditure has been found in island rails, ducks, pigeons, flying foxes and rodents due to reduction in size, flightlessness and the influence of food habits (McNab 1994). Even though a smaller M_b has been found in cats from the tropical and temperate islands, no significant decrease in BMR of these cat groups was measured. Cats from the tropical islands had a slightly, but not significantly higher BMR, with a high variance when BMR was plotted against M_b (Figure 2, R^2 =0.59). The R^2 of the regression indicates that just 59% of variance in BMR data can be explained by variance in M_b. As mentioned above, a high parasite infestation has been found in cats from the tropical islands, which could explain the higher basal values and high data variance. A study on resting energy expenditure (REE) on malaria infected children showed a 30% increase in REE (Stettler *et al.* 1992). However, the impact of this disease might be higher than in this case, where no significant difference in BMR was detected between cat populations. It is not possible to quantify the influence of parasite infestation on energy expenditure and a further study, correlating metabolic measurements and parasite infestation, needs to address this question. Nevertheless, no significant difference in BMR between the three climate groups has been found, which is consistent with Chapter 1, where no BMR difference between climate zones was detected.

This study concludes that no island or climate adaptation is evident in the cats M_b and BMR. It is appreciated that the sample size of the cat groups is very different (e.g. Dirk Hartog Island n= 13; tropical islands n= 87) and that this could influence the average body mass. However, at least for tropical cats it is apparent that their body mass is smaller compared to the mainland population and that the differences are likely to be due to variations in nutritional prey availability, possibly influencing the cats' early development.

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Relationship between daily body temperature and activity patterns of free-ranging feral cats

Abstract

This study aims to quantify the relationship between activity and T_b pattern of free-ranging feral cats. Daily rhythms of body temperature (T_b) and activity (distance travelled) of eight free-ranging feral cats were recorded via implanted body temperature loggers and Global Positioning System technology (GPS-radio collars), over a period of 14 days. Both variables showed circadian rhythmicity, with cats being more active and showing higher T_b-values during the night. Analysis of covariance (ANCOVA) was employed to quantify the relative effects of activity and time of day on T_b. Most variance in T_b was explained by time of day, while considerably less variation was explained by distance travelled. Most importantly, the correlation between distance travelled and T_b was significantly stronger during daytime than at night. Indeed, night-time T_b showed little fluctuation at all. Taken together, the results suggest that the circadian T_b rhythm is primarily generated by an endogenous oscillator. In other words, the T_b rhythm is not just a by-product of the activity rhythm, as T_b crosses the average mean before the activity rhythms and the acrophases (time of daily peak) of the T_b and activity rhythm lie 14 - 299 minutes apart from each other.

This study is the first to investigate the relationship of T_b and activity of free-ranging, undisturbed feral cats and it improves the knowledge of the quantitative relationship between both variables.

Introduction

Many variables have been shown to influence daily rhythmicity, two of which, locomotor activity and body temperature (T_b), have been extensively studied (Rusak 1981; Refinetti and Menaker 1992). The close temporal relationship between the rhythms of body temperature and activity could suggest a correlation, where an increase in metabolic heat production derived from the increase in locomotor activity might be responsible for the body temperature rhythm. In addition, these two rhythms were simultaneously studied in various species (Honma and Hiroshige 1978; Meinrath and D'Amato 1979; Refinetti and Menaker 1992; Brown and Refinetti 1996; De Coursey *et al*. 1998). Studies on humans showed that the temperature rhythm starts to rise several hours before awakening, therefore is phase advanced in relation to the activity rhythm (Wever 1980; Weizman *et al.* 1982). In other animals the relationship between these two rhythms was rarely systematically analysed (Refinetti 1997; 1999).

Consistent and simultaneous collection of activity and T_b data of free-ranging animals improves the understanding of the interrelationships among animal behaviour, physiology, and ecology. The use of Global Positioning System (GPS) technology allows the continuos collection of spatiotemporal data of free living, undisturbed animals and can further been used for evaluation of e.g. movement patterns, spatial distribution and activity (Long *et al.* 2007). Thermochron iButtons (Dallas Semiconductor) are small (ca. 3 g) data loggers that record temperature and real time, with the data collection interval to be programmed by the user. Although originally designed to monitor temperature of perishable goods during transportation, they are increasingly being used by animal physiologists to collect data of free-ranging or semi-captive individuals (Seebacher *et al.* 2003; Mzilikazi *et al.* 2004; Mzilikazi and Lovegrove 2004; Taylor *et al*. 2004; Laurila and Hohtola 2005; Masaki *et al.* 2005; Superina and Boily 2007; Warnecke *et al.* 2007; Lovegrove and Génin 2008; Schleucher *et al.* 2008; Hilmer *et al.* submitted).

The aim of this study was to combine the collection of activity and T_b of free-ranging, undisturbed feral cats, and to investigate and quantify their relationship with a possible future application of T_b rhythm as a surrogate for activity to interpret field data.

Materials and Methods

Study area

The study was conducted on Dirk Hartog Island, 850 km north of Perth. For detailed description of climate, habitat and coordinates see Chapter 6.

Trapping

Cats were trapped using padded leg-hold traps (Victor 'Soft Catch'® traps No. 3; Woodstream Corp., Lititz, Pa.; U.S.A.) with a combined lure system of a blended mixture of cat faeces and urine ('Pongo'). Cats were sedated with an intramuscular injection (0.2 ml) of Zoletil 100®, sexed, weighed, and inspected for trap injuries. After the examination, cats were brought back to the field station, placed into a holding cage of dimensions (800 x 300 x 300 mm) and kept in a quiet place, away from noise and direct sunlight. They were kept for a period of 2-4 days and were fed with commercial cat food and provided water ad lib.

Implantation of data loggers

Prior to implantation, body temperature loggers (iButtons) were calibrated (Chapter 4) and programmed to collect one data point at intervals of 10 minutes, starting two days after operation (see Hilmer *et al.* submitted). Implantations were conducted by an experienced veterinarian from Perth. Cats were initially sedated with an intramuscular injection containing a combination of 0.05 mg/kg Medetomidine hydrochloride (1mg/ml, "Domitor", Novartis Animal Health Australasia Pty Ltd.) and 0.3 mg/kg Butorphanol tartrate (10mg/ml, "Torbugesic", Fort Dodge Australia Pty Ltd). Five minutes later, an intramuscular injection of 6 mg/kg Ketamine hydrochloride (100 mg/ml, "Ketamil", Troy Laboratories Pty Ltd.)

was administered. When cats were well sedated, the veterinarian examined all cats for injuries again, to ensure only healthy cats were implanted with an iButton. The left flank of the cat was shaved and sterilized with chlorhexidine gluconate (Chlorhex S, Jurox Pty Ltd) and 95% ethanol. iButtons were soaked in chlorhexidine gluconate and ethanol for sterilization. After cleaning, an incision were made in the left flank and the sterilized iButton was wrapped in omentum and sewed in place with Dexon II sutures (polyglycolic acid sutures, size 0 [3.5 metric], "Dexon II", United States Surgical). The muscle tissue was then closed in individual layers (internal and external abdominal obliques) with Dexon II sutures and the skin closed intracutaneously with Dexon II sutures. Following the operation, all animals were injected subcutaneously with 0.3 mg/kg Meloxicam (5mg/ml "Metacam", Boehringer Ingelheim) and 75 mg of Procaine Penicillin (300mg/ml "Norocillin S.A. Injection", Norbrook Laboratories Ltd) for inflammation prophylaxis.

Preparation for release, release

While still under sedation, each cat was equipped with a GPS data logger radio collar with mortality and time-since-death signal (Sirtrack, New Zealand), factory programmed to collect a location fix every 10 minutes. Cats needed to weigh more than 2.1 kg to be able to be fitted with a 105 g radio collar (i.e. collar weight < 5% of body mass). Cats were then placed back in the holding cage and monitored to ensure normal awakening from sedation. The following morning, cats were released at the capture site and were monitored via VHF collars for a duration of three weeks.

Relocation of iButtons and GPS-collars

This study was part of a broader feral cat baiting exercise by the Department of Environment and Conservation (DEC), conducted three weeks after release of the collared animals. Following the baiting campaign, the cat carcasses were located; collar and T_b loggers were collected and brought back to Perth for data download and analysis.

Statistical analysis

Data of iButtons and GPS-collars were downloaded for each individual cat using download devices and software provided by the manufacturers. The T_b-values were corrected with the calibration difference, which was obtained through the calibration before the implantation. GPS data included date, time, latitude and longitude, number of satellites and horizontal dilution of precision (HDOP). The HDOP is the likely precision of the location as determined by the satellite geometry, which ranges from 1-100. (Sirtrack GPS Receiver manual, Sirtrack New Zealand). Fixes < HDOP 10 were excluded from the evaluation, because a correct location of the cat could not be assured.

Distance of two GPS fixes (in eastings and northings coordinates) were calculated, using Pythagoras' theorem, which states `in a right angled triangle, the square of the length of the hypotenuse equals the sum of the squares of the other two sides'. As Eastings lines are perpendicular with Northings, the theorem can be utilized to calculate the distance between the two points, using following formula:

$$d_{\text{(Distance)}} = \sqrt{\,} a^2_{\text{(Eastings)}} + b^2_{\text{(Northings)}}$$

Several missing activity values, mostly during the day time, due to unsuccessful GPS fixes, made the analysis of individual days impossible. Therefore, the data set was averaged to mean values at 10 minute intervals for the entire study period (14 days). Three methods were used to analyze the phase relationship between the two rhythms, body temperature and activity (distance travelled). The ascendance method uses the time at which the level of body temperature or activity crossed the mean level during its daily rise. For each animal, all 14 days of records were ‘educed’ into a single day by averaging each bin over the 14 days. The time at which the educed rhythm crossed the educed daily mean was taken as the ascendance phase-reference point for that animal.

The acrophase method involves the fitting of a cosine wave to each educed rhythm. The corresponding time to the peak of the best-fitting cosine wave was defined as the acrophase of the rhythm (Refinetti 1999; Piccione *et al.* 2002). Statistical analysis of ascendance phase- reference points and acrophase of body temperature and activity was conducted using unpaired t-tests (StatistiXL 1.8).

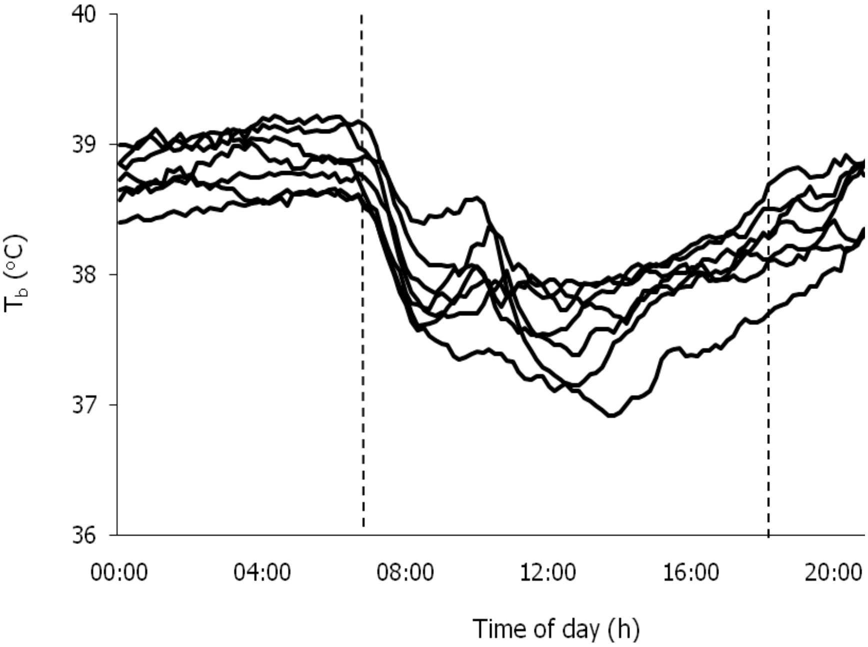
Analysis of covariance (ANCOVA) was used to analyse the influence of time of day (fixed factor with two levels: day/night) and activity (continuous covariate: distance travelled) on T_b (dependent variable). ANCOVA allows testing for the independent and correlated effects (interaction term) of both independent variables. Specifically, if any circadian rhythmicity in T_b were entirely caused by differences in activity levels, then the fixed factor ‘time of day’ as well as the interaction term should be non-significant, and only the covariate should have a statistically significant effect.

Results

Eight feral cats (five males 4970 ± 450 g, three females 3270 ± 590 g) were used in this study. Figure 1 shows the mean body temperature and activity rhythms of all eight free-ranging feral cats over the 14-day-observation period. Both variables showed a strong daily rhythmicity, with higher values during the night phase of the dark-light rhythm.

The influence of time of day (day/night) and activity (distance travelled) on T_b was tested using ANCOVA (Table 1). A highly significant influence ($P < 0.0001$) of time of day on T_b was found in seven cats, with one additional cat (B2) showing a P-value of < 0.003 (Figure 2). This was reflected by very high F-ratios for the fixed factor (time of day) (Table 1). Activity (distance travelled) had a weaker effect on T_b (as evidenced by considerably smaller F-ratios), with five out of eight cats showing a significant influence. In four cats a significant effect of the interaction term (time of day x distance travelled) on T_b was detected. The latter finding is indicative of different slopes for the correlation between activity and T_b during day- and night-time, with a strong increase in T_b with increasing activity levels during day-time, but almost invariable T_b–values during night-time (e.g. Figure 2 a, e, g).

Examples of educed rhythms of body temperature and activity of two cats are shown in Figure 3. The rhythms ascend and cross the daily mean around the time of sunset. Figure 4 shows the mean phase-reference points of body temperature and activity rhythms, as determined by the ascendance method, for all eight cats. The body temperature mean of six cats crosses the daily mean before sunset, whereas just one activity mean crosses the daily mean before and seven after sunset. No significant difference between body temperature and activity phase reference points could be detected ($P = 0.327$). The acrophase of T_b and activity of all eight animals occurred at similar times between 23:00-02:35 h, with one exception; the T_b acrophase of DH5_1 occurred at 0:05 h, whereas the peak of activity has been detected at 5:04 h. No significant difference between the acrophase of body temperature and activity phase reference points (*P* = 0.615, Table 2) were detected.



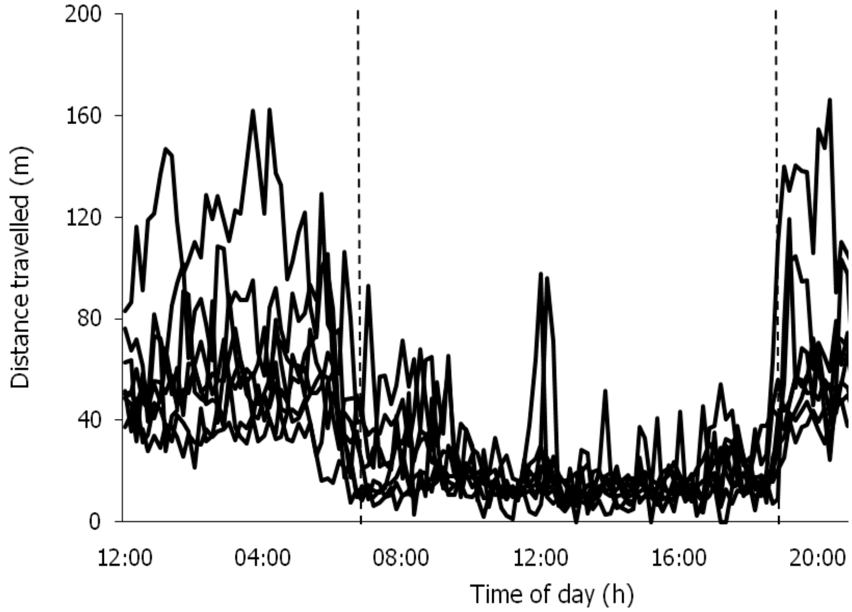


Figure 1. Mean body temperature and activity patterns of eight free-ranging feral cats, recorded over a period of 14 days. Vertical dashed lines indicate sunrise (06:35h) and sunset (18:25h).

Table 1. Results from ANCOVA analysing the relationship between day/night (fixed factor) and distance travelled (covariate) on body temperature (dependent variable). Significant effects are marked in bold typeface.

DH5 (a)	*df*	Mean Square	*F*	*P*
Time of day	1	2.24	41.92	**<0.0001**
Distance	1	0.38	7.11	**0.009**
Time of day x Distance	1	0.26	4.88	**0.029**
Error	140	0.05		

DH5_2 (b)	*df*	Mean Square	*F*	*P*
Time of day	1	1.24	15.00	**<0.0001**
Distance	1	0.41	4.96	**0.028**
Time of day x Distance	1	0.08	0.98	0.32
Error	140	0.08		

DH12 (c)	*df*	Mean Square	*F*	*P*
Time of day	1	5.03	61.05	**<0.0001**
Distance	1	0.38	4.56	**0.035**
Time of day x Distance	1	1.15	14.00	**<0.0001**
Error	140	0.08		

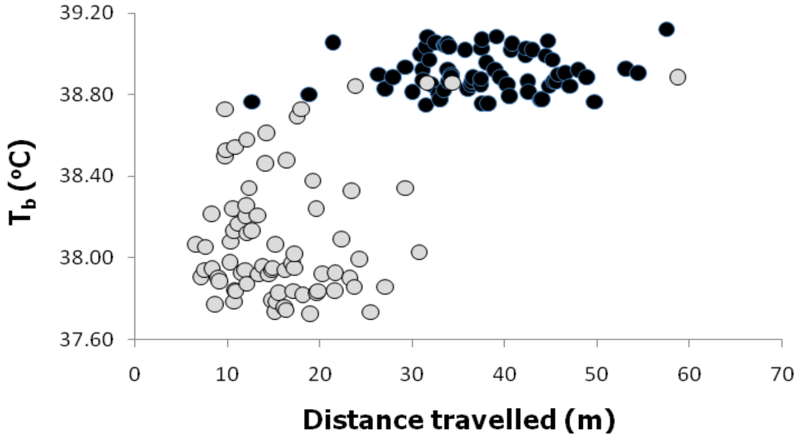
DH17 (d)	*df*	Mean Square	*F*	*P*
Time of day	1	1.30	22.40	**<0.0001**
Distance	1	0.27	4.61	0.33
Time of day x Distance	1	0.06	1.03	0.31
Error	140	0.06		

MB8 (e)	*df*	Mean Square	*F*	*P*
Time of day	1	3.29	94.94	**<0.0001**
Distance	1	1.64	47.25	**<0.0001**
Time of day x Distance	1	1.13	32.69	**<0.0001**
Error	140	0.04		

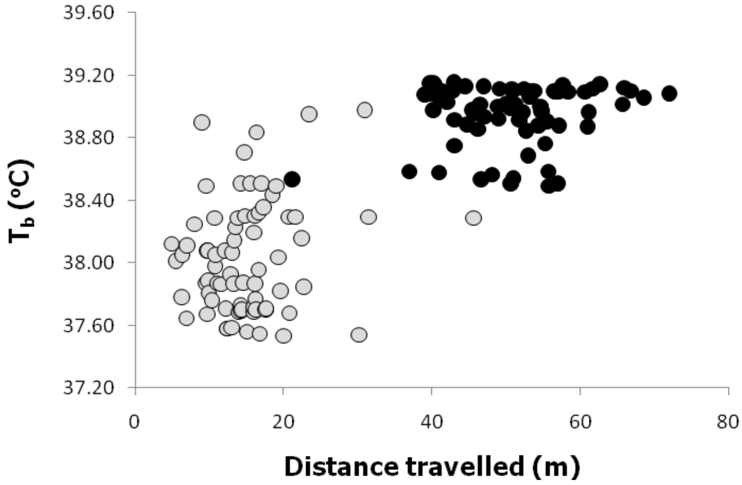
MB5 (f)	*df*	Mean Square	*F*	*P*
Time of day	1	2.93	20.72	**<0.0001**
Distance	1	1.13	7.98	**0.005**
Time of day x Distance	1	0.41	2.93	0.089
Error	140	0.14		

B2 (g)	*df*	Mean Square	*F*	*P*
Time of day	1	0.71	9.05	**0.003**
Distance	1	0.21	2.74	0.10
Time of day x Distance	1	0.01	0.17	0.69
Error	139	0.08		

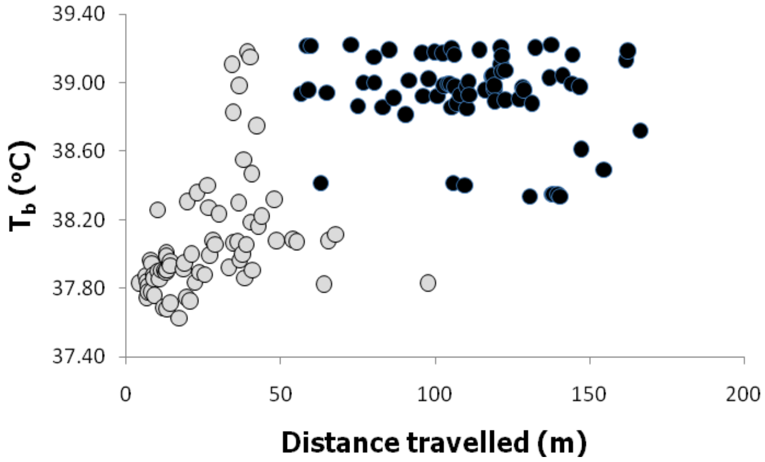
B3 (h)	*df*	Mean Square	*F*	*P*
Time of day	1	4.90	58.96	**<0.0001**
Distance	1	0.19	2.50	0.12
Time of day x Distance	1	1.03	13.36	**<0.0001**
Error	140	0.08		



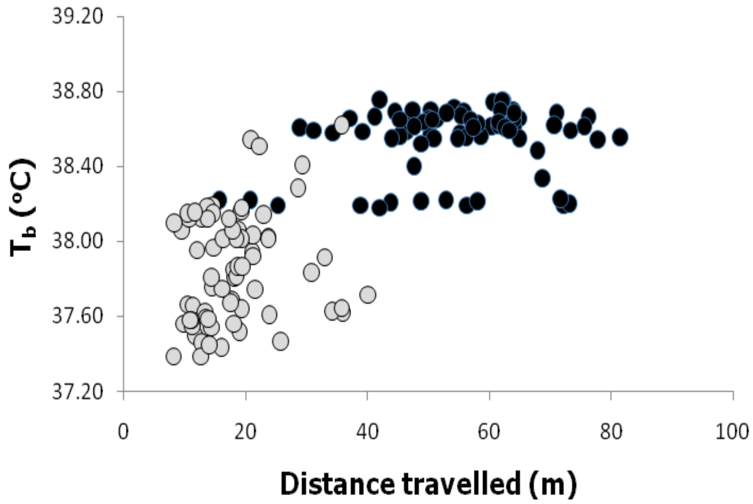
DH5 (a)



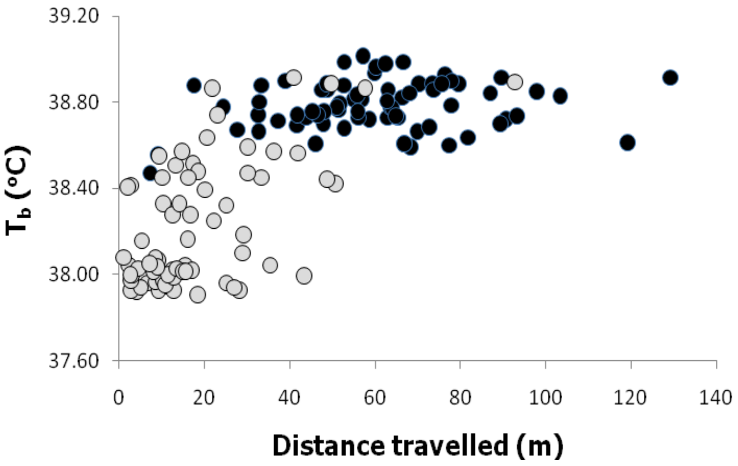
DH5_2 (b)



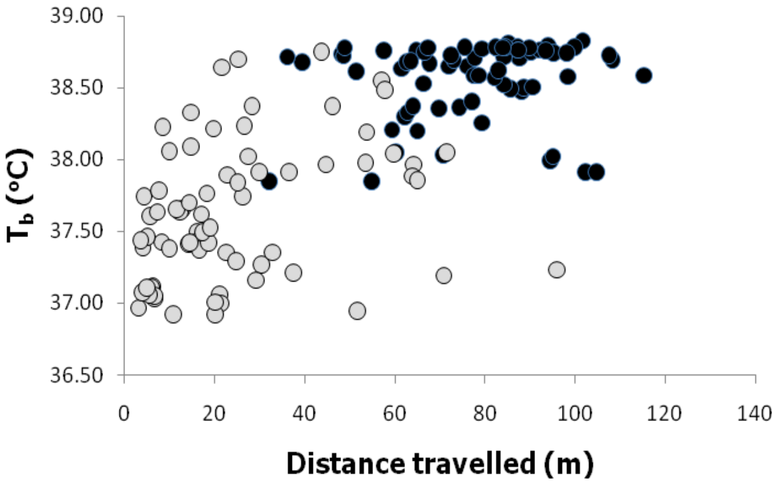
DH 12 (c)



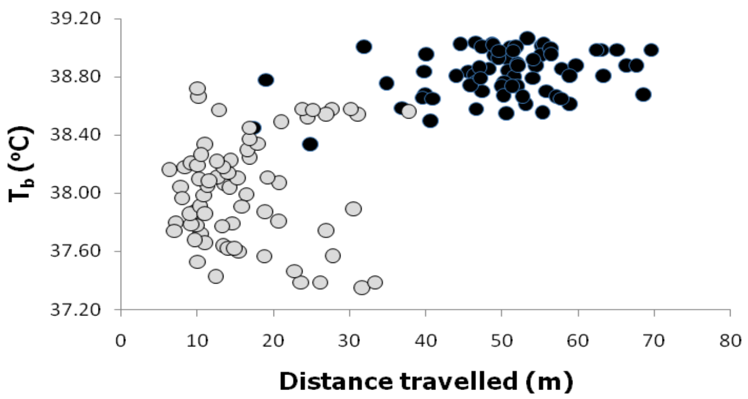
DH 17 (d)



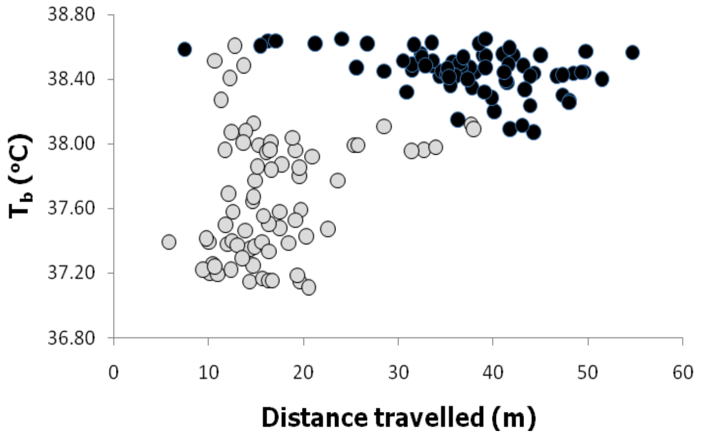
MB 8 (e)



MB 5 (f)

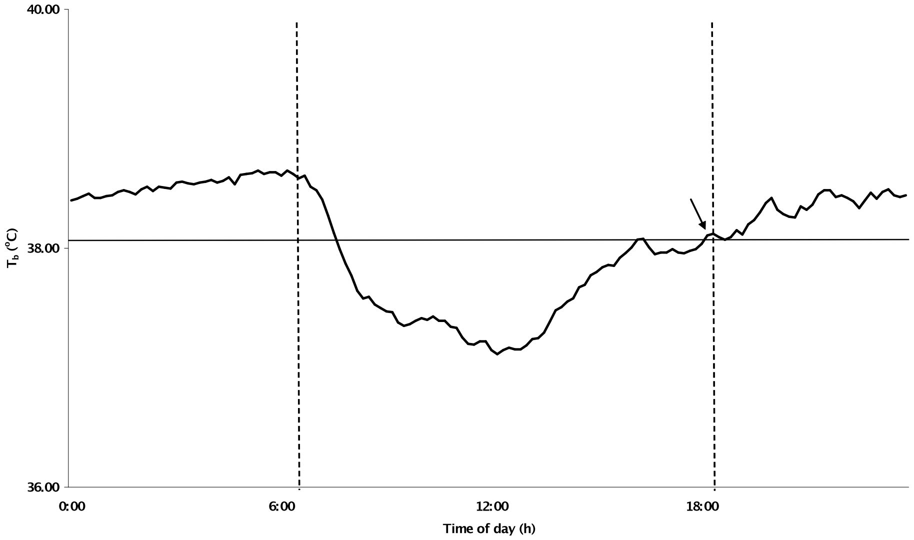


B2 (g)

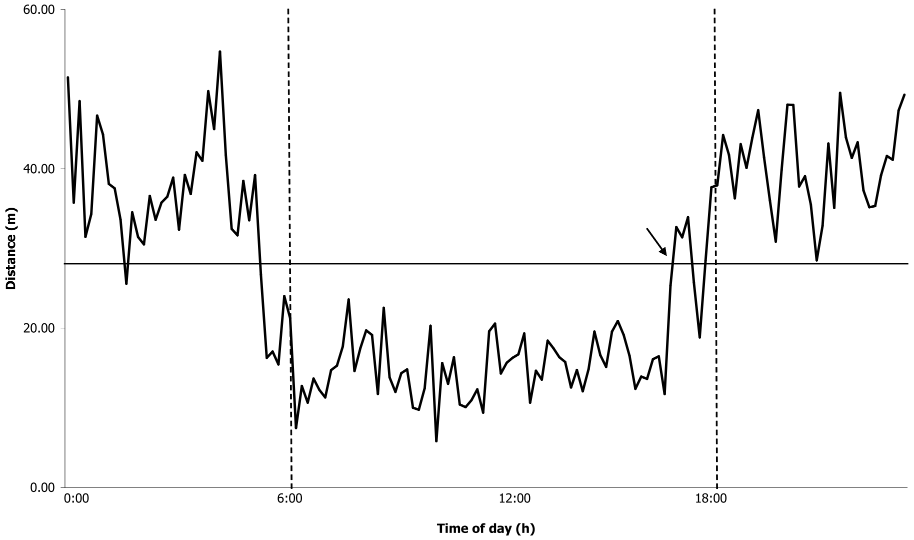


B3 (h)

Figure 2. Relationship between distance travelled (m) and body temperature (°C) of eight free-ranging cats at day (grey circles) and night (dark circles), determined by sunrise (6:35 hours) and sunset (18:25 hours).


40.00
38.00
36.00
T_b (°C)
0:00
6:00
12:00
18:00
Time of day (h)

A


60.00
40.00
20.00
0.00
Distance (m)
0:00
6:00
12:00
18:00
Time of day (h)

B

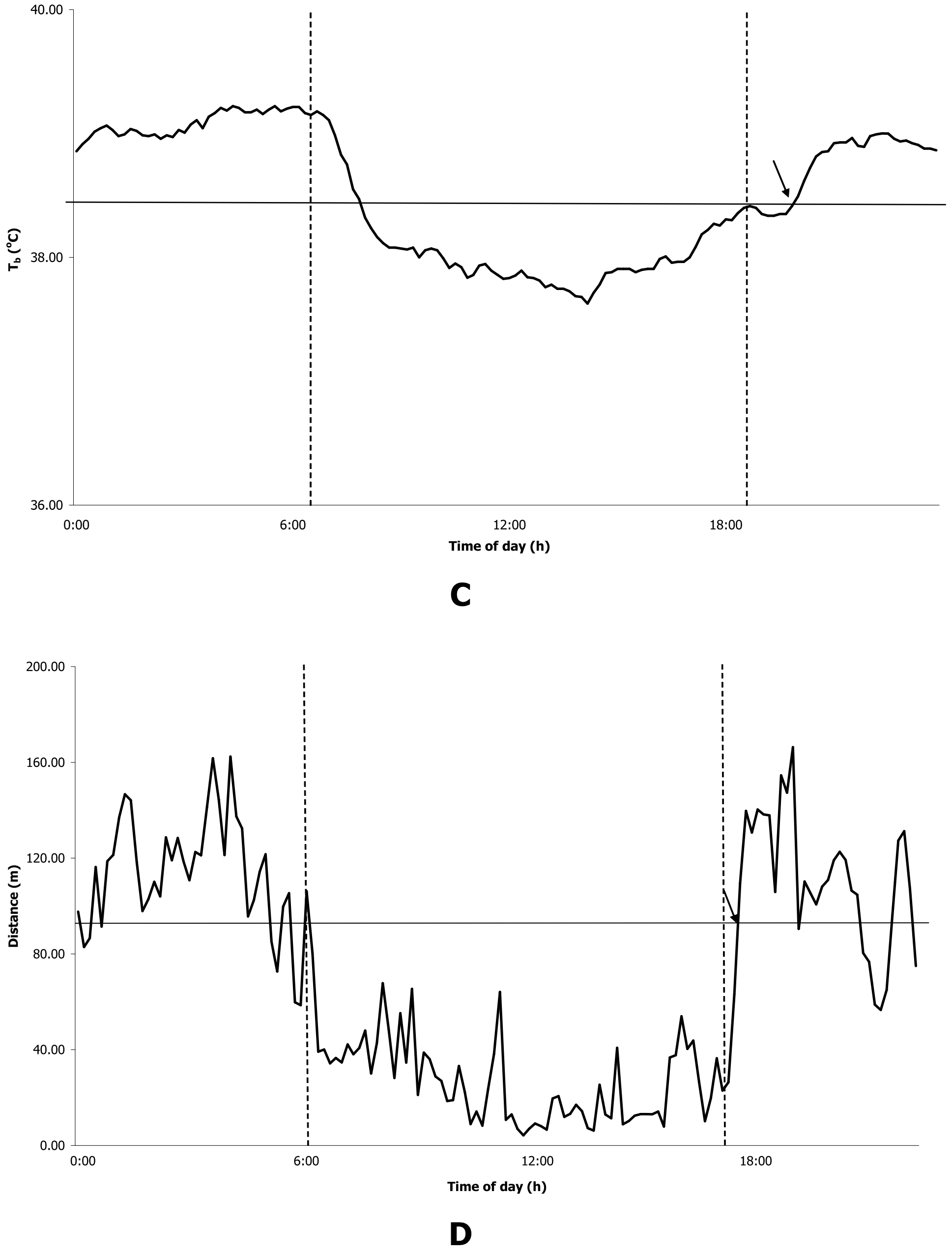


Figure 3. Educed rhythms of body temperature and activity (distance travelled) of cat B3 (A+B) and DH 12 (C+D) indicate sunrise (06:25 h) and sunset (18:35 h). Horizontal lines indicate means. The point at which the rhythm crosses the daily mean is indicated by an arrow. Note the different y scale in Figure B and D.

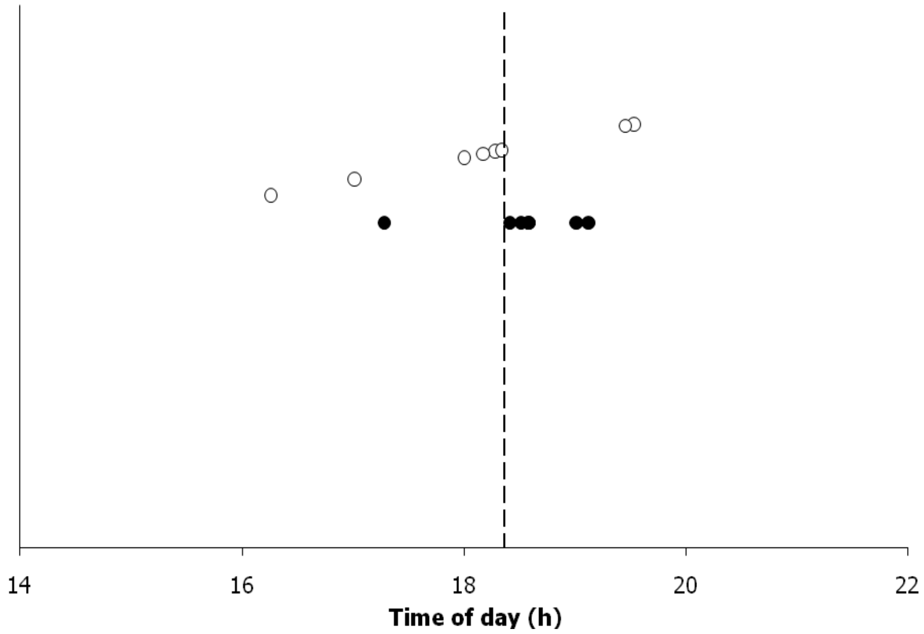


Figure 4. Mean phase- reference points for T_b rhythms (white circles) and activity (black circles) of eight free-ranging feral cats, determined by the ascendance method. Vertical dashed line indicates time of sunset (18:25 h).

Table 2. Mean phase- reference points for body temperature and activity rhythm of feral cats, determined by the acrophase method.

	Acrophase (hour)		
Cat ID	**T_b**	**activity**	**Difference between T_b and activity (minutes)**
B2	23:04	00:05	61
B3	0:45	23:02	103
DH12	1:05	00:51	14
DH17	0:58	01:19	21
DH5	0:22	00:45	23
DH5_1	0:05	05:04	299
MB5	2:35	01:43	52
MB8	2:14	01:22	52

Discussion

The results of this study show that both rhythms, T_b and activity, of free-ranging feral cats show a strong daily rhythmicity, with higher values occurring during the dark phase of the light-dark rhythm and lower values during the light phase. This is confirmed by acrophases between midnight and 05:00 h. These nychthemeral cycles are common in nocturnal mammals (Refinetti 1994, 1997, 1999; Warnecke *et al.* 2007) and it is consistent with my own previous findings, where a pronounced nocturnal T_b rhythm of free-ranging feral cats was detected (Chapter 4; Hilmer *et al.* submitted). The similar pattern of both rhythms could suggest a synchronisation, where locomotor activity produces heat, which increases body temperature. By quantifying the sensitivity of body temperature to changes in activity, a significant effect was found in five out of eight cats, with an increase in activity resulting in an increase of body temperature, consistent with several other studies (De Castro 1978; Franken *et al*. 1992; Refinetti 1994; Brown and Refinetti 1996; Weinert and Waterhouse 1998). Also, Hilmer *et al*. (submitted) found that free-ranging cats were mostly active during the night; however a few T_b-peaks around midday were also recorded. It was suggested that these T_b-peaks were most likely due to activity peaks caused by hunting, territory fights or long-distance movements. These suggestions from Hilmer *et al.* can now be confirmed by this study. Time of day however had the strongest (highly significant) effect on T_b, suggesting that the daily T_b rhythm is generated for the most part by an endogenous oscillator and that activity affects the T_b amplitude but does not determine the rhythm of T_b. This is most apparent during the cats' inactive phase (day-time), where an increase in activity levels results in an increase of T_b (Figure 2). During night-time, this effect is not discernible, possibly due to the independent, strong, endogenic T_b rhythm.

The results of the ascending and acrophase method also suggest that no close synchronisation of both rhythms is apparent, even though no statistical difference was found. The body temperature rhythm of seven out of eight cats ascends past the daily mean before sunset, whereas all except one activity rhythm ascend after sunset. The acrophase phase reference points of T_b and activity are more closely synchronized than the ascending method, with acrophases occurring between 23:00 and 05:00 h. However rhythm peaks of T_b and activity are still 14 - 103 minutes apart, except cat DH5_1, where T_b and activity peaks are ~ 5hours apart. This is not consistent with Refinetti's study (1999), who found that the mean phase reference points for T_b and activity of the ascendance methods of three nocturnal species cross the daily mean almost at the exact same time, at the transition between light and darkness. In addition, the acrophase of T_b and activity rhythm also showed very similar times of the phase reference points. But even though, a close synchrony between both rhythms was apparent, '*body temperature can not be taken as a by product of the activity due to higher body temperature rhythm during the active phase, irrespective of activity*'. This study agrees with Refinettis study, which states: '*while the activity rhythm might alter the amplitude and shape of the T_b rhythm, it does not cause it*'.

Chapter 4 describes the difference in T_b rhythm of free-ranging and captive feral cats, with an apparent decrease of T_b amplitude and robustness of captive cats. The lack of activity in captivity could be responsible for the decrease in T_b rhythm amplitude and robustness, described by Refinetti (2006). However, as mentioned in Chapter 4, it is not possible to quantify the factors mostly influencing the T_b pattern of captive cats, due to many variables changing when animals kept in captivity (e.g. activity, interaction with competitors, social behaviour, and food availability).

The lack of close synchrony of both rhythms in this study, compared to Refinetti's study (1999), is possibly due to two factors. Firstly, the priority of this study was to evaluate data of free-ranging, undisturbed animals. Therefore, Global Positing System (GPS) technology was employed, and distance moved between fixes was used as a representative for activity. By using GPS radio collars, a number of unsuccessful fixes during the day, due to cats sheltering in caves or burrows resulted in missing activity data (Chapter 6). Therefore it was decided to average the data set, using mean values, calculated over a period of 14 days, and not using each individual day for seven day average for the ascendance and acrophase method, like shown in Refinetti's study (1999). Consequently, this methodology possibly fails to show a close synchrony of both rhythms, described in other studies (Refinetti and Menaker 1993; Refinetti 1999). Secondly, free-ranging cats in this study were occupied in normal routine activities like hunting and socializing, including large distance movements, resulting in high activity peaks, especially during the night phase of the day/night rhythm (average movement of cats (n= 15) at night time: 4102 ± 413 m; day: 1219 ± 169 m (mean ± SE), Chapter 6). These intense activity peaks do influence the body temperature rhythm, as discussed above, however at this point it is not possible to quantify the relationship.

This study demonstrated two different ways of analysing the relationship of activity and T_b and I conclude that in this case, the analysis of covariance (ANCOVA) gives a stronger understanding about the correlation of both variables, whereas for the ascendance and acrophase method possibly a complete data set is essential, shown by Refinetti (2006). Even though this study had limitations in the data set, it gives valuable insight into the correlation of both variables. It confirms that the T_b rhythm is strongly influenced by time of day, generated by an endogenous oscillator and activity alters the T_b amplitude, with a T_b increase with an increase of activity. Furthermore, this study agrees with all other published data on the relationships of activity and T_b of mammals (except humans), stating that T_b cannot be taken as a sole by-product of activity. In addition, future studies on T_b rhythms need to be cautious in suggesting that high T_b is only caused by activity. The driving force of the internal oscillator affecting both parameters must be appreciated.

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Impact of long term captivity on metabolism and body temperature variation of the feral cat

Abstract

The impact of long term captivity on the physiology of cats was investigated by comparing the basal metabolic rate (BMR) and body temperature (T_b) variation of free-ranging versus captive feral cats. Cats kept in captivity for 12 months showed a significantly lower BMR than recently captured feral cats (21196 ± 4283 Jh^{-1} versus 33198 ± 11285 Jh^{-1}; $P < 0.01$). Free-ranging feral cats showed a pronounced daily T_b cycle with higher temperatures during the dark phase (39.22 ± 0.27 °C, light phase: 38.12 ± 0.47°C) and an acrophase (time of daily peak) between 22:30 - 23:15 h. In the course of captivity, mean body temperature levels (37.77 ± 0.34 ^{o}C) as well as minima and maxima (36-39 ^{o}C versus 35.5- 41.9°C, free-ranging cats) of three captive cats shifted towards a decrease in amplitude (T_b- amplitude: 0.629 - 0.957 °C). The rhythmicity changed with time in captivity from nocturnality to a diurnal tendency, with an acrophase between 12:00 - 16:25 h.

This study clearly shows that captivity affects BMR and T_b patterns in feral cats and therefore previously derived data from captive cats can not directly be applied to free-ranging populations.

Introduction

To date, more than 90% of data available on physiological parameters are derived from investigations under artificial laboratory conditions (Geiser *et al.* 2000; McKechnie and Wolf 2004). However, little information is available regarding the effect of long term captivity on physiological parameters, like metabolism and activity patterns, despite the fact that captive animals live in an artificial environment with different diet, lack of exercise and activity and adaptation to human handling.

Many factors have been suggested that may influence the level of energy requirements. Body mass (M_b) is generally acknowledged to be the most important factor setting the level of basal rate (BMR) in mammals (Kleiber 1932, 1961; McNab 1980, 2008). Also, various other factors have been suggested as determinants of BMR, including body composition, body temperature, climate, phylogeny, diet, habitat and life history (Hayssen and Lacy 1985; McNab 1986; McNab 2000; Munoz-Garcia and Williams 2005; Careau *et al.* 2007). Activity patterns of carnivores are also influenced by a number of factors, like daily temperature variation (Schmidt-Nielsen 1983), interaction with competitors (Carothers and Jaksic 1984), social behaviour (Ewer 1973), food availability (Boulos and Terman 1980; Zielinski 1988) and the own activity cycle of prey (Zielinski 1988). Nevertheless, only a few studies have considered captivity as a possible factor for physiological changes; even though, many of the above influencing factors might quite drastically change in captivity (O'Regan and Kitchener 2005). Some studies have proved that captivity impacts on the physiology of the animals studied (Warkentin and West 1990; Geiser and Ferguson 2001; Warnecke *et al.* 2007; Schleucher *et al.* 2008), whereas other studies were unable to find an effect (Larcombe and Withers 2007).

Data available on the metabolism and circadian rhythmicity of cats available in the literature (Kane *et al*. 1981; Heusner 1982; Johnson and Randall 1985; Randall *et al.* 1987; Lovegrove 2000; McNab 2000b; Riond *et al.* 2003; Wichert *et al.* 2007) are all derived from captive, domestic cats. Free-ranging cats do not appear to have been investigated with regard to their metabolic physiology or activity patterns. This study focuses on the comparison of BMR and circadian rhythmicity of free-ranging versus captive cats, with the aim of quantifying the potential influence of captivity.

Material and Methods

Metabolic measurements

Six adult feral cats (1 male, 5 females mean mass 3633 ± 393 g) were captured at Mt Keith (27°16'S120°31'E), located in the Gascoyne region of Western Australia. The climate is characterized by summer and winter rain, the annual precipitation is 200-250mm (for habitat details, see Chapter 1). Cats were transferred to the Department of Environment and Conservation (DEC) research centre, Perth, and housed individually in outdoor pens (5x3x2m) with shelter provided. The cats were kept on a varying diet of canned cat food or fish (feeding time: 12:00-14:00 h) with one starve day per week and water was supplied ad libitum. Contact with the animals was restricted to feeding time.

The basal metabolic rate of the cats was measured once after six and 12 months of captivity at an ambient temperature of 28 °C (Thermal neutral zone, Hilmer 2005; Schleucher *et al.* 2008). To evaluate the period of basal metabolic rate, a minimum of 30 minutes of the lowest metabolic reading was used and the mean value of this period was calculated. Lowest readings were recorded between 20:00-24:00 h. Data were compared to the BMR of recently captured cats also at Mt Keith (lowest reading 20:00-3:00h, Chapter 1).

Experimental set-up

Metabolic rates were measured via indirect calorimetry by using a one-channel oxygen analyser (Servomex 572B, measuring range 0 – 100 Vol. %, accuracy ± 0.1%), which was calibrated against pure oxygen and nitrogen (see review by Withers 2001). Re-calibration was conducted at the beginning and end of each experiment against ambient air. Instrument output was read by a voltmeter

(Voltcraft VC 840), which transferred the data through an RS 232 interface to a PC for data collection. Gas volumes were corrected for air pressure fluctuations and reduced to STPD (standard temperature and pressure, dry). Cats were placed in a metabolic chamber with a clear plexiglass front (50 x 40 x 44 cm). A second exit was installed at the rear of the chamber to enable removal of the cat without direct handling.

Pre-dried room air (silica gel with non-toxic humidity indicator) was pressed through the chamber by an adjustable membrane pump (Type: WISA) at a rate of 550 L h^{-1}. Flow rates were constantly monitored via a flow meter (Rota Yokogawa, L 742 11484, 40-630 L7h; Rota Yokogawa, 860806.4403; 0.16-10L/h). Outgoing chamber air was passed through a drying column of Silica gel and via bypass. 8 L h^{-1} were sampled by a second pump (WISA) and passed through a set of three drying columns (Silica gel/ Drierite ($CaSO_4$)). Humidity was constantly monitored by a humidity probe (Hygrotest 80, Testoterm GmbH & Co., Lenzkirch) in an airtight container in the air stream, and then passed through a fine filter before entering the analyser. The metabolic chamber was placed in a controlled temperature cabinet (Arcus 400E, Australia Ltd Perth 140x 60x 65 cm, accuracy ± 1 °C), which was set to an ambient temperature of 28 ^{o}C. The first hour of measurement was discarded from any data analysis.

Measurements were started between 08:00 h and 09:00 h and finished the next day at 07:00 h. On experimental days, cats were not fed prior to capture or during the duration of the measurements. Cats adjusted quickly to the experimental protocol, and exhibited no indications of stress.

Analysis of body fat

To determine if the body fat changes with time in captivity, five recently captured cats and six cats kept in captivity for 12 months were humanely destroyed and frozen carcasses were minced several times (sieve dimensions: 15 mm and 4 mm) with an industrial mincer. The tissue samples were sent to the chemistry centre Perth, where the total fat percentage of each cat was analysed with a Soxleth extraction (Luque de Castro and García-Ayuso 1998).

Body temperature data collection

Body temperature (T_b) measurements were taken from three captive (for details of holding and feeding procedure, see above) and three free-ranging cats. Data loggers (iButtons, DS 1921H Thermochron iButton, Dallas Semiconductor/Maxim, Dallas, Texas, USA, accuracy ± 0.12 °C) were calibrated before insertion, in a water bath to ± 0.1°C at 5 °C increments over the range 5 to 40 °C, against a mercury-in-glass thermometer traceable to a NATA (National Association of Testing Authorities) calibrated standard. iButtons were programmed to commence recording two days after surgery to avoid recording any postoperative effects on T_b (for details, see Warnecke *et al*. 2007; Hilmer *et al.* submitted).

Free-ranging cats were captured at Lorna Glen Station, (arid zone, 180 km ENE Wiluna, Western Australia, 26°13.6S 121°326E). Data loggers were implanted by a veterinarian on site (Hilmer *et al.* submitted). While sedated, cats were equipped with a VHF radio collar with mortality and time-since-death signal (Sirtrack, New Zealand). Cats were released at the site of capture after one day of recovery and not disturbed for the period of measurement. iButtons recorded T_b every 30, 40, 60 min (total recording time 43, 56, 85 days). After a poison-baiting exercise, cat carcasses were located via VHF radio collar and the iButtons collected from cats were read with the iButton reader and associated software program. Data of free-ranging cats were compared to T_b data of cats held in captivity for 12 months (Data recorded every 10 minutes, Data collection 14 days).

Statistical analysis

Basal metabolic rate

Values are given as mean ± standard deviation with sample size (n), significance level was 0.05. Analysis of variance (ANOVA) with Student-Newman-Keuls test was used to identify differences in BMR and body mass (M_b) between captive and recently captured cats. The effect of body mass on BMR was determined by linear regression (StatistiXL 1.8).

Body mass and Body fat

An unpaired t-test was used to test for significant differences in body mass and total body fat of the cat populations (StatistiXL 1.8).

Circadian Rhythmicity

Mean T_b of all cats was defined by light and dark phase, determined by sunrise and sunset of the two study sites. The Cosinor program (Refinetti 1993: http://www.circadian.org/softwar.html) was used to calculate cosinor parameters: mesor (mean level), amplitude (half the range of excursion) and acrophase (time of the daily peak). For calculation of the acrophase, the days of data were first averaged for each animal. Cosine waves were then fitted to the averaged 24h rhythm. The corresponding time to the peak of the best-fitting cosine wave was taken as the acrophase of the rhythm (Piccione *et al.* 2002). The robustness or stability of a rhythm was also calculated by the Cosinor program. This program calculates ratios of variances for various possible periodicities. The highest ratio indicates the true period at a significant statistical level. These statistics reflect the strength or regularity of a rhythm independently of its amplitude (Refinetti 2004).

Results

Basal metabolic rate

BMR changed significantly over the period of captivity (*P* = 0.013, Table 1, Figure 1) with recently captured animals having the highest BMR (33198 ± 11285 Jh^{-1}). After six months in captivity, the BMR showed a non-significant decrease (24897 ± 1684 Jh^{-1}; *P* = 0.067). BMR decreased significantly after twelve months in captivity, compared to recently captures cats (21196 ± 4283 Jh^{-1}; *P* < 0.01) but not compared to cats captive for six months (*P* = 0.168).

Table 1. Body mass (M_b) and basal metabolic rate (BMR) of recently captured, 6 and 12 months captive cats at TNZ (28 °C).

recently captured cats		**6 months captivity**		**12 months captivity**	
M_b(g)	BMR (Jh^{-1})	M_b (g)	BMR (Jh^{-1})	M_b (g)	BMR (Jh^{-1})
3900	22230	3950	22752	4600	27048
3400	27982	3500	24325	4000	23800
3000	28320	3150	23625	3500	23730
3500	35490	3400	26316	3600	18936
3400	30668	3250	25805	3650	16097
5000	54500	3400	27098	3600	17568

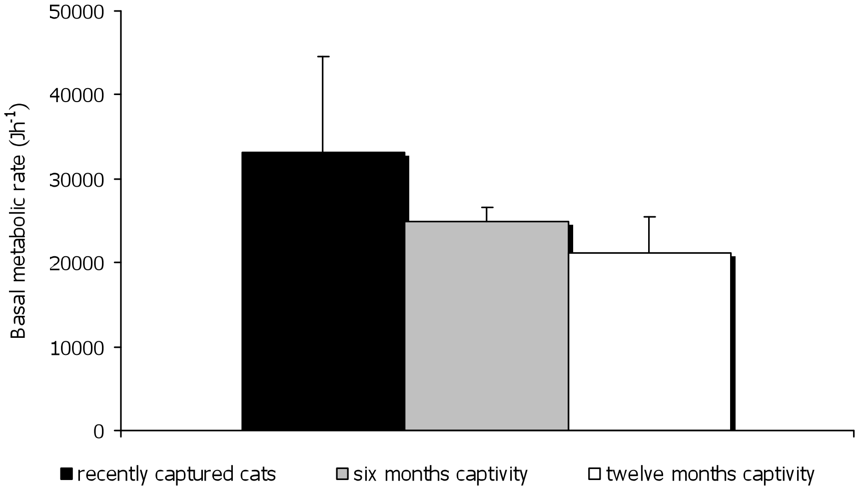

Figure 1. BMR (+ SD) of 6 feral cats in the course of a 12-months captivity period at ambient temperature (T_a) representing thermoneutrality (28 °C).

Body mass and body fat composition

The mean M_b of the study animals was 3655 ± 494 g (Table 2; P = 0.382) and M_b was not significantly influenced by captivity. The total body fat significantly changed with time in captivity, doubling from 7 to 14.2% body fat (Table 3; P <0.0001). Data from a recently captured cat (18% body fat, marked in grey in Table 3) was excluded from the evaluation as it was captured at a mine waste disposal site, exposed to an unlimited food source, whereas the other cats were captured away from the settlement, independent of human food, relying entirely on hunting 'natural' prey.

Table 2. M_b (g) of the three cat populations studied.

Body mass (g)		
recently captured	**6 months captivity**	**12 months captivity**
3900	3950	4600
3400	3500	4000
3000	3150	3500
3500	3400	3600
3400	3250	3650
5000	3400	3600

Table 3. total body fat percentage of recently captured cats and cats kept in captivity for 12 months. Note that the value marked in grey* has been excluded from the evaluation.

Total body fat % of recently captured cats	Total body fat % of cats held in captivity for 12 months
6%	15%
(18% *)	16%
5%	14%
10%	14%
7%	14%
	12%
Mean: 7%	**14.2%**

Body temperature

The mean T_b of three free-ranging cats (LG 1-3) was 38.7± 0.67 ^{o}C (n= 42-83 days), with a T_b range between 35.5- 41.9 °C. T_b of the cats showed a pronounced daily cycle of body temperature, with significant (*P* <0.0001) higher T_b in the dark phase and lower T_b during the daytime (Table 4, Figure 2, 4). The acrophase (time of the daily peak) of the three free-ranging cats varied from 22:34 h (LG 2), 22:57 h (LG 1) to 23:17 h (LG 3), with a daily T_b amplitude between 0.77-0.98 °C. Circadian period was found to be 24.0 h for all three free-ranging cats with the robustness of the circadian rhythm varying from 21.4% (LG 3), 33.6% (LG 1) to 59.8% (LG 2). In the course of captivity, mean T_b levels (37.77± 0.34 °C) as well as minima and maxima (36-39 °C) of the three captive cats (MtK 3-5) shifted toward a decrease in amplitude (0.629-0.957 °C). Less robust rhythmicity was detected (1.7%, MtK 4; 2.2%, MtK 3; 5.2%, MtK 5, Figure 3, 5), with significant T_b difference between dark and light phase (Table 4) and the period of the rhythm (23.8 ± 0.05 h) was slightly but significantly shorter ($P = 0.03$), with the acrophase varying from 12:00 h (MtK 4), 12:23 h (MtK 3) to 16:25 h (MtK 5).

Table 4. Mean T_b of free-ranging (LG 1- LG 3) and captive cats (MtK 3-5) ± SD of dark and light phase (defined by sun rise and set) with t-Test results of dark-light comparison for each cat.

Cat I.D.	**Mean T_b dark phase**	**Mean T_b light phase**	**P**
LG 1	39.25 ± 0.29	38.12 ± 0.48	$P < 0.0001$
LG 2	39.06 ± 0.32	37.86 ± 0.58	$P < 0.0001$
LG 3	39.34 ± 0.20	38.39 ± 0.35	$P < 0.0001$
MtK 3	37.38 ± 0.15	37.57 ± 0.16	$P < 0.0001$
MtK 4	38.06 ± 0.133	38.20 ± 0.19	$P < 0.0001$
MtK 5	37.59 ± 0.25	37.95 ± 0.14	$P < 0.0001$

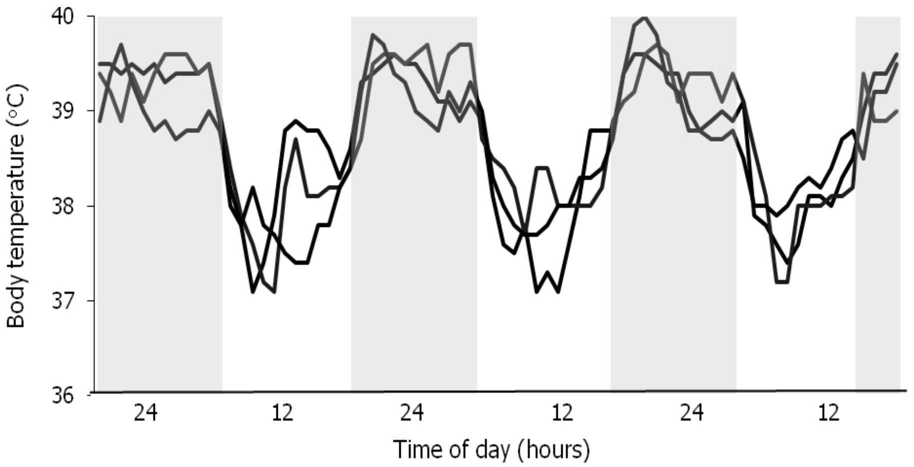

Figure 2. T_b of three free-ranging feral cats on three consecutive days. The dark bars indicate periods of darkness (18:40-07:10 h).

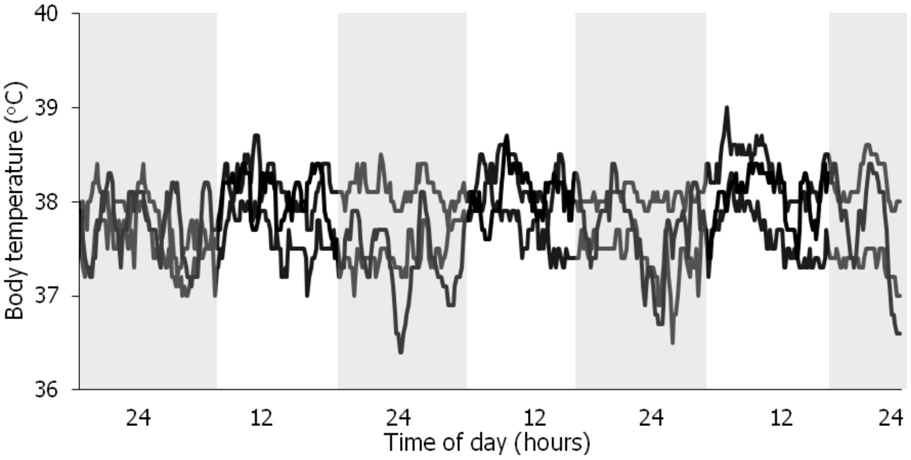

Figure 3. T_b of three captive feral cats on three consecutive days. The dark bars indicate periods of darkness (18:00 -06:40 h).

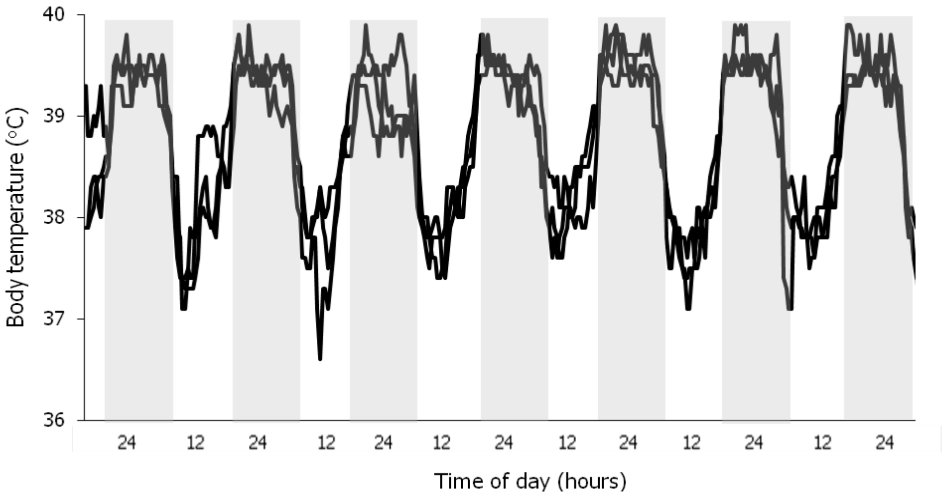

Figure 4. Body temperature of one free-ranging cat (LG1) on three consecutive weeks. Note the pronounced daily rhythm, higher during the dark phase, indicated by the dark bars (18:40-07:10 h).

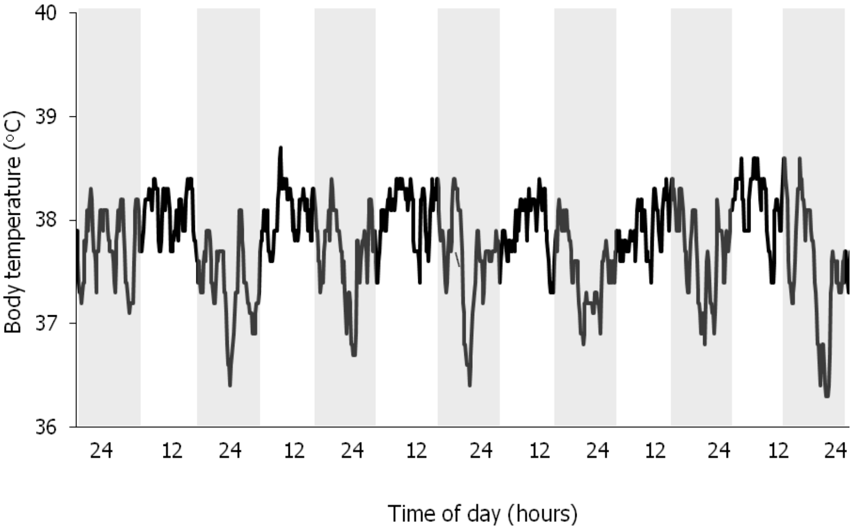

Figure 5. T_b of one captive cat (MtK 5) on seven consecutive days. The dark bars indicate periods of darkness (18:00 -06:40h).

Discussion

The results of this study show that captivity significantly influences the two measured physiological parameters, basal metabolic rate and T_b variation, in feral cats. Recently captured cats, caught in the wild and measured the same night, showed the highest basal metabolic rate. This may be due to a potential difference in stress levels between cats contributing to the large standard deviation shown in Figure 1. Nevertheless, cats were observed to settle down quickly in the metabolic chamber and engaged in comfort behaviour like resting and sleeping. Cats kept in captivity over a period of 12 months and measured twice in that time, showed a distinct decline in BMR over that period. The handling of the cats was limited to feeding times to minimize habituation towards humans. After several months however, a change in behaviour was observed, with cats being more calm and tame around humans and in the experimental set up. Therefore, part of the decline in BMR could be explained by relaxation in the metabolic chamber.

Two neurophysiological studies (Cannon *et al.* 1929; Ring *et al.* 1931) that quantified the influence of the sympatric nervous system on energy demand and thermoregulation provide the only data in the literature comparable with the data presented in this study. Unfortunately, the authors do not report key details of experimental setup and protocol (Duration, time of day, nutritional status etc.). Thus it is uncertain whether the results reflect basal metabolic rates. Surprisingly, the measurement of BMR of domestic cats has not been revisited since these two studies but their data have been used by other authors for comparative purposes and BMR allometric relationships (Heusner 1982; McNab 2000). Recent studies have provided data on the daily energy requirement of domestic cats but not on the BMR (Martin *et al.* 2001; Edstadtler-Pietsch 2003; Riond *et al.* 2003). McNab (2000) compared the standard energetics of nine Felidae species and one Hyaenidae family. He stated that cats (*Felis catus*) have a 127% higher BMR than that expected from an all-mammal curve. He also concluded that the BMR in most Felids is higher than generally expected from body mass, using the all mammal-curve (McNab 1988). However, he suggests that the diversity among Felids in size, habitat, climate and behaviour is great and that overall conclusions about energy requirements should be viewed cautiously. This study supports his suggestions, with a significant difference in BMR being demonstrated between wild and captive feral cats.

The metabolic adjustments to captivity are most likely to be driven by several differences between the natural and captive environment. A change in body composition due to lack of activity and exercise could lead to a reduction in the mass of metabolically active muscle tissue and an increase of metabolically inactive fat tissue. Without doubt, the activity level of the cats decreases substantially in captivity compared with their activity in the wild as active hunters, engaging in regular hunting, involving stalking, running and killing (Dickman 1996; Bradshaw 2006). O'Regan and Kitchener (2005) summarized the effects of captivity on mammalian morphology and concluded that restricted activity levels appear to have a great effect on captive animals with an increase in the amount of subcutaneous and deposited fat. This is consistent with the result of this study, which found a significant increase in body fat from seven to 14.2% in one year. Nevertheless, these results are still lower than the total body fat percentage of stray cats, captured at a waste disposal site, south of Perth, Western Australia (28%, Müller 2006). When comparing the body fat percentage of domestic cats in the literature, values of up to 50% total body fat are reported (Hawthorne and Butterwick 2000), suggesting that the cats in this study are still in a healthy, non-obese state. It is unlikely that the food availability to the captive feral cats is comparable to domestic housecats that have unrestricted access to food and excess treats and scraps.

Another major difference between the natural environment and the artificial environment of captivity is the availability and quality of food (McKechnie *et al.* 2006). Variations in intestine length within a species have been found to change with quantity and quality of food in relation to energetic demands of animals (Moss 1972; Gross *et al*. 1985; Green and Millar 1987; Korn 1992; Al-Mansour 2005). When feeding cats commercial cat food, up to 93% of the available digestive energy would be expected to be metabolized (Kendall *et al*. 1982), whereas a study on feral cats on the Galapagos Islands showed an energy digestibility of diet categories varied from 50% (e.g. grasshoppers, beetles, arachnids) to 85% (rodents). Despite mammals representing the most important prey species of feral cats, invertebrates like grasshoppers can become locally important when other prey species become scarce (Paltridge *et al*. 1997). Hence, we could hypothesis that the intestine length of feral cats in captivity decreases due to the predictable and highly nutritional food supply which is reflected in the significantly reduced BMR after one year. Free-ranging feral cats on the other hand possibly need longer intestines in favour of maximum digestive efficiency of food of lower digestive value. Studies on mammals have indicated that a large part of BMR is generated by the brain and by the organs in the abdominal cavity (Aschoff *et al.* 1971; Schmidt-Nielsen 1990). It has been proposed that in carnivores a short gut incurs the cost of lower digestive efficiency but it is an advantage for hunting due to the reduced body weight (Houston 1988). The wildcat (*Felis silvestris*), known as a facultative specialist (Moléon and Gil-Sánchez 2003) specializing on high energy digestible prey species like rabbits and other rodents, has a shorter intestine compared to domestic cats (Daniels *et al*. 1998). Nevertheless no data is available regarding changes of intestine length in cats with change in quality of food and work needs to be done to test this proposed hypothesis.

Previous investigations of activity patterns of domestic cats showed diverse results. Several studies (Hawking *et al.* 1971; Mugford and Thorne 1980; Kane *et al.* 1981; Macdonald and Rodgers 1984; Riond *et al.* 2003) were unable to find a circadian rhythm, whereas others found a significant T_b rhythm in cats (Johnson and Randall 1985; Randall *et al.* 1987), which has been described as diurnal (Szymanski 1919), nocturnal (Mcdonald and Apps 1978) or polycyclic (Lucas and Sterman 1974; Randall *et al.* 1987). The results of this study suggest that captivity may influence circadian rhythms in cats. Free-ranging, undisturbed cats showed a distinct robust circadian rhythm (21-59.8%), with higher T_b in the dark phase (39.2 °C), and a steep body temperature drop before sunrise, with significant lower T_b during the light phase (38.1 °C, $P < 0.001$). Cats held in captivity for one year, decreased the robustness (1.7-5.2%) of the circadian rhythm and most strikingly, the cat's activity pattern shifted from nocturnal to diurnal-tendency, with the acrophase shifting from around midnight (free-ranging cats) to midday (12-16 h). This result is combined with a decrease in T_b amplitude and T_b patterns during the light and dark phase. The mean T_b of the two study groups ranged between 37.77 °C for captive cats and 38.7 °C for free-ranging cats, which is on the lower and upper level of published values (37.9-38.4 °C, Johnson and Randall 1985; Kuwabara *et al.* 1986; Randall *et al.* 1987). However, this comparison should be taken cautiously, because all available data on mean T_b of cats have been collected from domestic cats in a controlled environment, with controlled ambient conditions and food supply, whereas free-ranging cats were highly active hunters (maximum T_b of 42 °C) and exposed to ambient temperatures ranging from -2 to 41 °C. The circadian rhythm of most mammals is not free-running; it is influenced by factors such as the light-dark rhythm, ambient temperature and food availability (Refinetti 2006). The nyctohemeral rhythm of cats is likely not just related to the circadian rhythm, but might also reflect an increase in endogenous heat production resulting from time of activity. Mc Nab and Morrison (1963) stated that '*in most studies of physiology activity is considered only as an undesirable complication to be eliminated, or at least, reduced to a minimum'*. It is, however, impossible to manipulate the activity of free-ranging cats, and yet collect data from undisturbed animals in their natural environment.

By examining the mean T_b patterns of all three free-ranging cats, a bimodal waveform, with two distinct peaks before dusk and dawn is visible, which has been discussed in the literature as a common waveform for activity in animals (Aschoff 1966; Refinetti 2006) and also specifically in the cat (Randall *et al.* 1987). An increase in T_b is apparent in the late afternoon with T_b crossing the daily mean T_b level before sunset (Figure 4). A higher body temperature is visible during the dark phase, which is reflected in the acrophase around midnight. This rise of T_b in the late afternoon could be due to hunting diurnal prey species, like reptiles, birds and also rabbits, which when present, represent the major part of the food source of cats (Dickman 1996; Molsher *et al.* 1999). Also, the free-ranging cats showed a few peaks in T_b around midday (Hilmer *et al.* submitted), which could be explained by a potential territory fight, a period of hunting or a long distance movement during the day, which has been recorded for nocturnal wolves (*Canis lupus*) (Merrill and Mech 2003). However, these high T_b during the early phase of the light phase has just been observed three times in all three free-ranging cats. The activity pattern of feral cats has been described in the literature as 'being active at any time; they are usually more active at night, with the two periods of greatest activity centred near the times of sunrise and sunset' (Reagan 1994). Being active during the cooler night, the cat avoids the heat of the day to conserve water and to avoid overheating. Also, mammalian predators are known to synchronize their predatory activities with the activity of their prey (Curio 1976; Zielinski 1988). The cats prey consist of diurnal (reptiles, birds) and nocturnal prey (mammals) and studies on feral cat diet suggest, that mammals represent the major prey of feral cats; however they also prey on other animal groups, depending on abundance and seasonal availability (Jones and Coman 1981; Dickman 1996, Koch *et al.* submitted).

When wild feral cats are taken into captivity, changes occur in the various factors likely to influence the natural T_b pattern, such as interaction with competitors, the social behaviour and the food availability. On the other hand, new potential influencing factors are introduced, including a daily feeding regime at midday, disturbance during the day from humans and unfamiliar noises and a restricted activity and exercise area. At this point it is impossible to quantify the factors mostly influencing the T_b pattern of captive cats, and only a descriptive discussion of the data is possible. The distinct day-night rhythms of free-ranging cats change when they are kept in captivity, with not just a decrease in T_b amplitude but also a shift to a diurnal active phase (acrophase between 12:00-16:00 h). Shifts in activity have been observed before in other animals such as the degu (*Octodon degus*), where diurnal activity shifted to nocturnal activity when they were given unrestricted access to a running wheel (Kas and Edgar 1999). Another example where a shift in activity has been observed occurred when one competitor, the nocturnal common spiny mouse, was removed from an area and the normally diurnal golden spiny mouse became nocturnal. This response suggests that the golden spiny mouse is pushed into the diurnal niche due to competition for limited resources (Shkolnik 1971).

In the study described here, it is unclear, why captive cats shift towards a diurnal activity. Perhaps a reduction in the stresses associated with hunting, socializing and competing for territory and partners could be part of the answer. Warnecke *et al.* (2007) found in their study that the robustness of the circadian rhythm in captive animals is much weaker compared to free-ranging animals. The circadian periodicity of southern brown bandicoots (*Isoodon obesulus*) decreased with time in captivity, which was attributed to a change in behaviour in captivity (eg. foraging time is reduced due to a highly nutritious food in captivity) and hence their physiology. Captive cats were exposed to a natural light-dark rhythm and were fed daily between 12:00-14:00 h. Randall *et al.* (1987) stated that cats are easily disturbed by humans and most of the studies on circadian rhythms of cats involve daily interruption for care and cleaning, which generate ‘false rhythms’. The comparison of T_b-pattern of free-ranging versus captive cats is difficult without the same controlled environmental conditions (imposed light-dark rhythm, controlled ambient temperature etc.). Nevertheless, differences in rhythmicity are established and noted and they give a valuable contribution to the number of studies discussing the impact of captivity on physiology of animals (Dawson and Carey 1976; Weathers *et al.* 1983; Warkentin and West 1990; Geiser *et al*. 2000; Geiser and Ferguson 2001; McKechnie *et al*. 2006; Larcombe and Withers 2007; Warnecke *et al.* 2007).

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Comparison of basal metabolic rate values of feral cats, with the latest study on standard energetics for Felidae

Abstract

Physiological studies aim to compare one particular species with a predicted value, calculated from a linear allometric equation from other species. This study compares basal metabolic rate values (BMR) calculated in this thesis, measured under different conditions (free-ranging and captive populations) with those from the most recent study on the standard energetics of Felidae. Captive cats in winter and summer showed a 74% and 59% of predicted BMR calculated from the allometric equation for Felidae. BMR value of free-ranging cats in summer was 93% of the closest value to prediction, whereas the BMR value for free-ranging cats in winter show 119% of prediction. All four cat groups however, are within the 95% prediction limits for an additional datum from the relationship for the other species. Therefore statistically, the BMR is not significantly lower than expected for an equivalently sized Felidae species. Nevertheless, this comparison showed the importance of evaluating and quantifying differences in season and captivity, for allometric relationships and comparison of physiological data to ensure a correct interpretation of data.

Introduction

Body mass has a major allometric effect on most physiological variables including basal metabolic rate (BMR) (Kleiber 1932; Withers 2000; White and Seymour 2003, McNab 2009). Also other determinants of BMR have been widely discussed in the literature including body composition, body temperature, climate, phylogeny, diet, habitat, seasons, life history and the animals' personality (Heldmaier and Steinlechner 1981; Hayssen and Lacy 1985; McNab 1986, 2000; Li and Wang 2005; Munoz-Garcia and Williams 2005; Careau *et al.* 2007). BMR is a repeatable measure of the minimal rate of energy expenditure under standard conditions by endotherms (McNab 2000). Standard least-squares regression (Y = a + bX, where a = intercept, b = slope, x = body mass, Y = physiological variable) is generally used in comparative studies of several species to determine the linear relationship between body mass and a physiological variable. The regression indicates the statistical significance of the relationship and provides variance estimates for both the intercept (a) and the slope (b). It also provides predictive statistical use, e.g. the 95% confidence band for the regression is often calculated and shown graphically to indicate the goodness of fit (Cooper and Withers 2006). Once an allometric relationship has been established, it is possible to determine whether a new species conforms to this relationship and conclude whether factors such as physiological adaptation of a species can be performed (Lovegrove 2000; Withers *et al*. 2000; Schleucher 2002). This comparison however, should only be undertaken if differences in energy expenditure are due to physiological dissimilarity between species and not due to different experimental conditions such as difference in thermal neutral zone (TNZ), duration of experiment or feeding during the experiment. This is difficult to guarantee if data has not been derived from the same author and under the same standard experimental conditions. Several studies are available reviewing physiological parameters from previous published values with or without taking the differences in data collection into perspective (Elgar and Harvey 1987; Reynolds and Lee 1996; Lovegrove 2000; McNab 2000; White and Seymour 2003; McKechnie and Wolf 2004).

This study compares the findings from this thesis with the most recent study on the standard energetics of Felidae (McNab 2000). McNab compared the energy expenditure of 11 species of the family Felidae and found that the basal energy requirements of nine species were higher than for general mammalian standards and concluded that mammals that just eat vertebrates have higher basal rates. Nevertheless, 89% of McNab's data were derived from captive individuals, and did not include any information about the time of year when measurements were conducted. For cats we can be certain that a simple application of BMR, without including information about captivity state and seasonal measurement, should not take place and this will be discussed in context with McNab's allometric equation for Felidae (2000).

Material and Methods

BMR values

Chapters 1 and 3 demonstrated a significant difference in basal energy requirement between seasons and with time in captivity and therefore these effects will be compared to McNab's `standard energetics of mammalian carnivores: Felidae and Hyaenidae' (2000). Data from these chapters will be used for comparison (free-ranging winter and summer, captive winter), as well as one calculated value for summer captivity. A 36% decline in BMR was found when cats were kept in captivity for a period of one year. This study was conducted in the winter, data on BMR reduction in captivity in the summer was not available and therefore, a 36% reduced BMR was calculated from the free-ranging summer values and this value was used for comparison (see Table 1).

Table 1. mean M_b (g) and BMR (Jh^{-1}) data of three cat groups measured in this study and one calculated value (captive cats summer) from the results of Chapter 3, with a 36% reduction in BMR in one year captivity, measured in the winter.

Cat group	mean M_b (g)	mean BMR (Jh^{-1})	Source
Free-ranging cats winter	3700	33198	Chapter 1, 3
Captive cats winter	3825	21196	Chapter 3
Free-ranging cats summer	3446	24365	Chapter 1
Captive cats summer	3446	15594	calculation

Statistical analysis

Standard least-squares regression was used to determine the relationship between log-transformed mass and BMR for the family Felidae and 95% prediction confidence limits were calculated for the data set (for more information see Cooper and Withers 2006). Data from this study were included in the data set and if the new datum (e.g. BMR of cats in captivity in summer) was outside these 95% prediction limits, then it would be defined as being significantly different (0.05 significance level). The prediction limits are considerably broader than the confidence limits for the regression line which indicate the range within which the regression line falls at the desired probability level. The difference (in percentage) between the measured values of cats was calculated using the allometric equation for the family Felidae (McNab 2000).

Results

A significant allometric regression equation for 11 species of the family Felidae was BMR (Jh^{-1}): 38.9 M_b $^{0.8}$ (R^2: 0.92). Three of the four BMR data sets of this study fell below the prediction from mass, with the BMR of captive cats in the summer, showing the lowest BMR with 59% (15594 Jh^{-1}) of expected from mean body mass (3446 g). BMR of captive cats in winter was 74% (21196 Jh^{-1}) of expected from their mean body mass (3825 g) and the BMR of free-ranging cats in summer was 93% (24365 Jh^{-1}) of the prediction from mass (3446 g). BMR of free-ranging cats in winter on the other hand was 119% (33198 Jh^{-1}) of expected from mass (3700 g). All four data sets fell inside the 95% prediction limits of the regression (Figure 1).

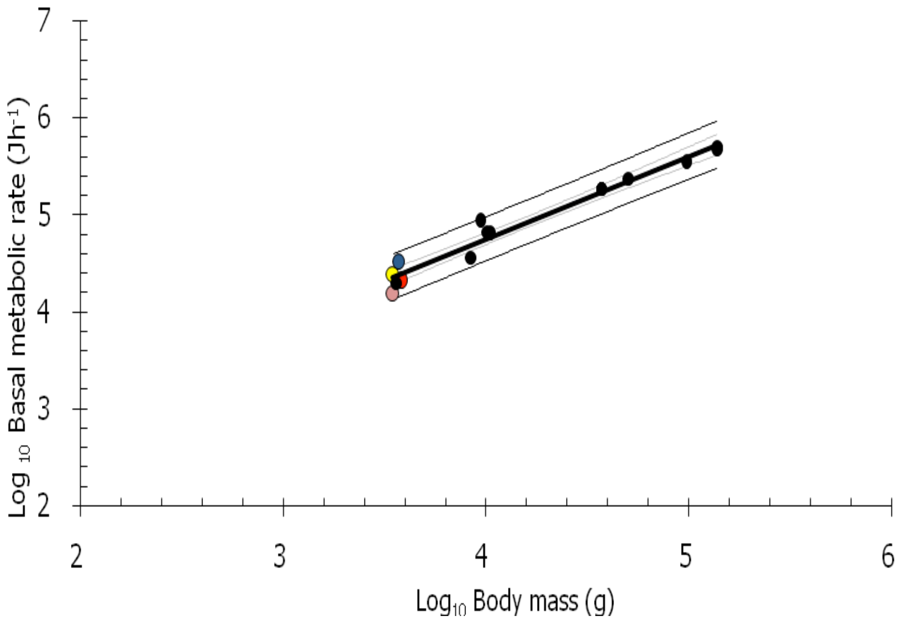

Figure 1. The relationship between mass (g) and basal metabolic rate (BMR; Jh^{-1}) for 11 Felidae species (black circles, McNab 2000), including the mean BMR value of free-ranging cats measured in summer (yellow circle) and winter (blue circle), captive cats measured calculated for summer (purple circle) and measured in winter (red circle) (log scaled). The regression line and the 95% prediction limits for predicting a further datum are indicated by a dark lines and the regression 95% confidence limits by grey lines.

Discussion

One of the aims of comparative physiological studies is to determine if a particular species, with a distinctive suite of life history and ecological characteristics, differs in their physiology from prediction, based on linear allometric regression for other species. In the past, several studies interpreted a physiological variable for a species (e.g. BMR) with an approximate value to be high (somewhat greater than 100% of the prediction) or low (somewhat under 100% of prediction) or to be expected (around 100%) (Peinke and Brown 2003; Song and Wang 2003; Mathias *et al.* 2004; Williams *et al.* 2004). Cooper and Withers (2006) challenged this approach, which is not based on any formal statistical analysis, and presented a statistical method for obtaining the 95% prediction confidence limits for regressions for comparison with a new species value. This statistical comparison was applied in this study, with the BMR of all four cat groups falling into the 95% prediction limits. Therefore, statistically, the BMR is not significantly lower than expected for an equivalently sized Felidae species, using McNab's (2000) allometric equation for Felidae as a comparison. However, as Cooper and Withers (2006) concluded, it is statistically difficult to demonstrate that a single species is significantly different from an allometric equation, due to a relatively low power for a single (new) species comparison. Nevertheless, it cannot be ignored that three of the four data sets were below (59%, 74% and 93%) and one 119% above the expected value from body mass. This intraspecific difference in BMR shows the importance of considering, in this case, season and captivity into the evaluations and that, at least for feral cats, an easy 'cause and effect' cannot be applied. Eighty-nine percent of Felidae species investigated in McNab's study were captive individuals and the season when he obtained his data is unknown. McNab acknowledges that most laboratory measurements on carnivores are obtained from captive-bred individuals, due to anxiety of freshly caught animals in a confined metabolic chamber. In the case of wild caught feral cats, a rapid relaxation occurs whilst in the metabolic chamber (personal observation) and the first hour of measurement was excluded from the study to ensure recording of only resting/basal metabolic rates. In many instances, the experimental animals needed to be awoken at the end of a measurement, which suggests total relaxation of the individual. Nevertheless, it is appreciated that it is not easy to catch large and dangerous wild lions (*Panthera leo)* or pumas (*Puma concolor)* to measure their metabolic rate. Results from this study, however, suggest that a strict dividing of data obtained from captive and wild caught individuals needs to take place to guarantee a correctness of comparison of allometric equations. McNab argued that Anderson *et al.* (1997) did not find a significant difference in standard energy expenditure of the African aardwolf (*Proteles cristatus)*, and therefore combining data was adequate. However, McNab overlooked the study from Mautz and Pekins (1989), where the BMR of captive bobcats (*Lynx rufus*) was measured, resulting in a 65% higher BMR (145987 Jh^{-1}) compared to McNab's BMR value for recently caught bobcats (88633 Jh^{-1}). The experimental set up of Mautz and Pekins' study could be disputed because ambient temperatures in the experiment were changed every three hours, which possibly affected the measurement of an exact BMR. Nevertheless, it demonstrates that a difference in BMR between captive and wild caught individuals exists and it also shows that an easy translation of captive versus wild animals is not possible. For feral cats we can say that the BMR decreases significantly in captivity. However a simple generalisation of increase or decrease or no change of BMR with time in captivity is not applicable and more emphasis should be placed on investigating the 'captivity effect' discussed in Chapter 4.

McNab (2000) used in his study eleven Felidae species, from which he measured nine species himself and obtained two values (*Felis catus*, Benedict 1938 and *Leptailurus serval*, Downs *et al.* 1991) from the literature. Benedict, however did not measure the BMR of cats himself, he used values, measured in the 1920's (Canon *et al.* 1929; Ring *et al.* 1931), where the metabolic rate of cats was measured as a by-product within a study mainly focusing on neuro-physiological experiments. Essential information regarding the duration and temperature in the experiment as well as body condition of cats are missing, and yet these values have been used in several basal energetic allometric comparisons (Benedict 1938; Kleiber 1961; Heusner 1982; Withers 1992; McNab 2000). The cats in this study show a 41% (captive summer) and 23% (captive winter) reduced BMR as compared to Benedict's data. One would assume that Benedict's animals were not subjected to standard conditions (not in the TNZ, not post absorptive), and it is likely the animals were under stress during the neuro-physiological experiment. It is understandable that published data will be used for comparisons, rather than measuring each species again, especially when studies compare physiological data for numerous species (e.g. Elgar and Harvey (1987) n=265; Lovegrove (2000) n=487; Lovegrove (2003) n=267; Lovegrove (2005) n=71, McNab (2009) n= 533), however, data should be viewed with caution. McKechnie and Wolf (2004) quantify these problems in their study, '*good prediction of allometry needs good data* '. They evaluated a study from Reynolds and Lee (1996), widely used today to predict avian BMR, and concluded that a significant proportion (181 of 248) of the data set used did not meet the criteria that define BMR or had a sample size less than three. When re-analysing the data set that met the criteria of BMR and a sample size of or greater than three, a significantly lower BMR was found than that obtained from Reynolds and Lee's original data set. Seven out of nine data points of McNab's data set have a sample size of three or less, with just two data points established from a sample size of four. Benedict (1938) published only one BMR value for a 3 kg cat, which McNab used in his data set and four servals were studied by Downs *et al.* (1991). Consequently, eight out of 11 data points were obtained from a sample size of three or less individuals. The total sample size studying this PhD on the other hand, was 37 individuals, with at least six individuals (except one data set) in any one study group. It is appreciated that a long term PhD can obtain more data than a study, designed to answer one specific question. Also McNab stated that it is difficult to work with large carnivores and that just a limited number of individuals are available for measurements. It is however questionable, how reliable McNab's data of just two or three individuals are, with Careau *et al.* (2008) proposing that the animal's personality plays an important role in energy metabolism. Hyperactive and exaggerated stressed individuals could respond with higher activity levels or greater muscle tonus, which could result in a higher metabolic rate (MR), compare to relaxed, calmer individuals. Even though just the lowest readings during a measurement are used for evaluation, it cannot be excluded that possibly one out of two or three animals never settles down during the experiment and therefore a higher MR will be recorded as the suggested BMR. This is however difficult to prove, and at this point, it is just noted, that a larger sample size than 2 or 3 would be more favourable to establish an exact BMR.

This study concludes that allometric relationships are fundamental in identifying metabolic adaptation of endotherms. However, this comparison should only be undertaken if differences in energy expenditure are due to physiological dissimilarity between species and not due to different experimental conditions. It is essential to emphasize the use of high quality data, with standardized experimental set up and a good sample size. For cats, data on captive and wild individuals as well as data on different seasons need to be separated and the data analysed and interpreted apart.

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Activity and home range sizes of feral cats on a semi-arid island off the coast of Western Australia

Abstract

Fifteen feral cats were trapped on Dirk Hartog Island in March 2009 and equipped with GPS (Global Positioning System) collars, to evaluate movement patterns and home range sizes. Home ranges of male cats tended to be larger (MCP 95: 10.7 ± 6.7 km^2; MCP 50: 3.9 ± 2.44 km^2, n= 11) than those of females (MCP 95: 7.1 ± 5.98 km^2, MCP 50: 3.26 ± 3.3 km^2, n= 4), however no significant difference could be detected, possibly due to the uneven sample size (t-test: MCP 95 $P = 0.717$, MCP 50; $P = 0.69$). The feral cats had widely overlapping home ranges (49.14 ± 7.01%) and core areas (53.6 ± 7.32%), suggesting a high degree of tolerance to other individuals. This was possibly due to high prey abundance and therefore potentially less competition pressure. Furthermore, results indicate higher activity during the night, with a significantly smaller distance travelled during the day (1219 ± 170 m) compared to night time (4102 ± 413 m). This was associated with a significantly lower percentage of fixes collected via the GPS-collar during the day (68.5 ± 5.9%), compared to night time (88.1 ± 4.5%; $P < 0.01$) possibly due to cats sheltering under bushes and in caves, impossible to collect a successful GPS fix.

Introduction

The cat (*Felis catus*), the world's most widespread terrestrial carnivore species, has been distributed throughout the world wherever humans have colonized. Cats occur on most of the world's islands (Long 2003), with deleterious impacts on endemic land vertebrates and breeding bird populations (van Aarde 1980; Moors and Atkinson 1984; King 1985; Veitch 1985; Bloomer and Bester 1992; Bester *et al.* 2002; Keitt *et al.* 2002; Pontier *et al.* 2002; Blackburn *et al*. 2004; Martinez-Gomez and Jacobson 2004; Nogales *et al.* 2004). Many studies on feral cats have been conducted, mainly on diet and impact on wildlife (see 'Overview of the feral cats on Australian native fauna'; Dickman 1996) but also on social structures and home ranges. These home range studies have mainly been on urban and farm cats (Liberg 1980; Jones and Coman 1982; Turner and Mertens 1986; Page *et al*. 1992; Denny *et al*. 2002; Meek 2003). A smaller number of studies have focussed on feral cats (Edwards *et al.* 2001; Burrows *et al.* 2003; Molsher *et al*. 2005; Moseby *et al.* 2009), indicating diverse home range sizes. Information about home range size and movement patterns are of importance for the design and refinement of control programs, to ensure the removal of resident cats and confine immigration of neighbouring cats into buffer zones (Edwards *et al.* 2001).

Dirk Hartog Island, Western Australia's largest offshore island, provides a unique study site, with feral cats being the main terrestrial predator. Feral cats became established on Dirk Hartog Island during the late 19th century and were probably introduced by early pastoralists. The island formerly supported at least 13 species of native mammals of which only three species still persist (Baynes 1990, McKenzie *et al.* 2000). Today, feral cats are common across the entire island and a successful eradication program would be essential for the reconstruction of the original fauna.

The aim of this study was to examine inter-individual variation in home range and the overlap of home ranges, and movement patterns of feral cats on the island.

Materials and Methods

Study area

This study was conducted in March - April 2009 on Dirk Hartog Island, 850 km north of Perth (25°50′S 113°0.5′E). The program was conducted on the northern third of the island, comprising of an area of approximately 250 km^2 (Figure 1). The island lies in the Shark Bay World Heritage Property and is the largest island off the Western Australian coast at 620 km^2 (Abbott and Burbidge 1995). The main vegetation complex across the majority of Dirk Hartog Island is spinifex (Triodia) hummock grassland with on overstorey of *Acacia coriacea*, *Pittosporum phylliraeoides* over *Acacia ligulata*, *Diplolaena dampieri*, *Exocarpus sparteus* shrubs over Triodia sp., *Acanthocarpus preissii* and *Atriplex bunburyana* hummock grasses, chenopods or shrubs. Adjacent to the western coastline is mixed open chenopod shrubland of Atriplex sp., *Olearia oxillaris* and Frankenia sp. and slightly inland in more protected sites, *Triodia plurinervata*, Triodia sp., *Melaleuca huegelii*, *Thryptomene baeckeacea* and Atriplex sp. There are small patches of bare sand across the island. In some areas there are a few birridas (salt pans). On the east coast there are patches of mixed open heath of *Diplolaena dampieri*, Myoporum sp. and Conostylis sp. shrubs (Beard 1976). The climate of the region (Peron Peninsula) is described as 'semi-desert Mediterranean' (Beard 1976; Payne *et al*. 1987), receiving an average of approximately 224 mm of rainfall annually with most of the rain occurring historically during May-July with annual minimum and maximum temperatures of 12-32 °C (Bureau of Meteorology).

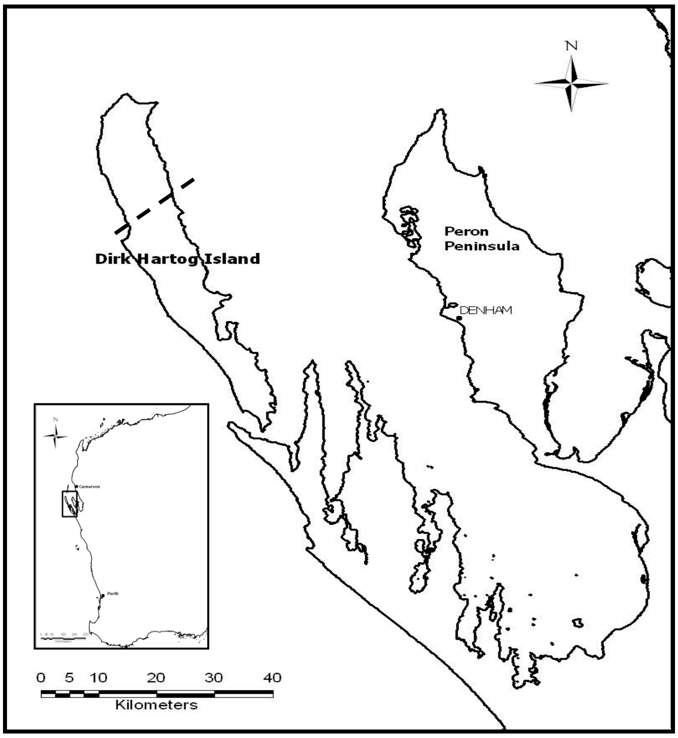

Figure 1. Study area; dashed line presents southern boundary of study area.

Trapping and Radio Collaring

Cats were trapped using padded leg-hold traps (Victor 'Soft Catch'® traps No. 3; Woodstream Corp., Lititz, Pa.; U.S.A.) with a lure system consisting of a blended mixture of cat faeces and urine ('Pongo') (Algar *et al.* 2002). Traps were located at 500 m intervals along existing roads/tracks (Figure 2). Trapped cats were sedated with an intramuscular injection of Zoletil 100® and then sexed, weighed, and inspected for trap injuries. After the examination, cats were brought back to the field station and placed into holding wire cages (800 x 300 x 300mm). They were kept in a quiet place away from noise and direct sunlight. Half of the cats were kept for a period of four days for a separate study, which included implantation of body temperature loggers (see Chapter 3). Cats were required to weigh more than 2.1 kg to be able to be fitted with a 105 g radio collar (less than 5% of body mass). They were provided with commercial cat food and water ad lib.

While sedated, cats were equipped with a GPS data logger radio collar with mortality signal (Sirtrack, New Zealand), factory programmed to take a location fix every 10 (n=8), 40 (n=6) and 80 (n=2) minutes (Table 1). Cats were then placed back into the holding cage and monitored to ensure normal awakening from sedation. The following morning cats were released at the site of capture and were monitored using the VHF function of radio collars over a period of three weeks. The mortality mode of the collar would start, if the cat did not move for a period longer than 24 hours.

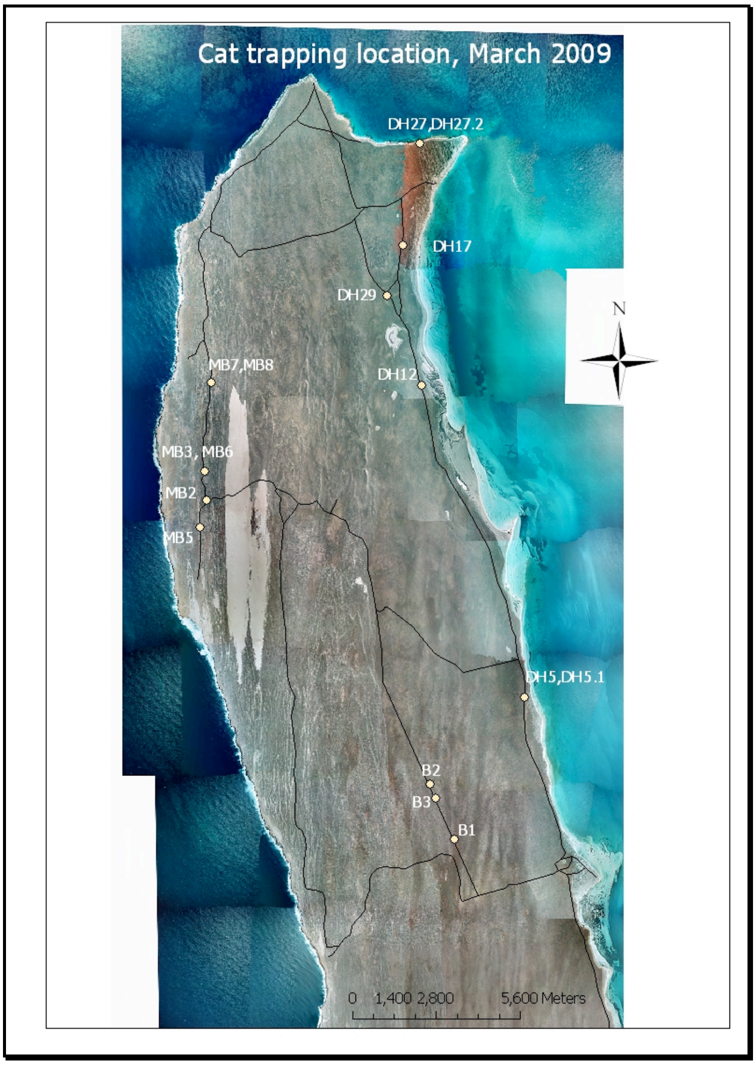

Figure 2. Location of trapped cats in March 2009.

Data collection

This study was conducted in concert with a feral cat baiting program conducted by the Department of Environment and Conservation (DEC) that occurred three weeks after the release of the cats. Immediately prior to the baiting program, cat GPS-positions were plotted from fixes obtained from an aircraft (Figure 3). Following the death of individual animals, the collars were retrieved.

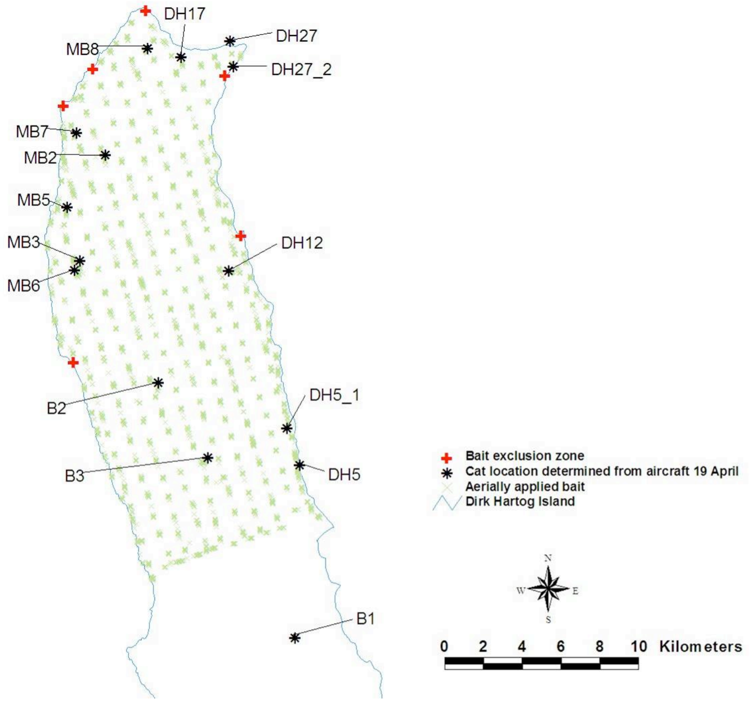

Figure 3. Map showing locations of collared feral cats as determined from an aircraft the day of baiting. Note that B1, outside the baited zone, was found dead before the baiting, course of death is unknown. DH29 was not located from aircraft, and therefore it is missing from the map.

Data Analysis

Data from the GPS-collar were downloaded with a download device and software program, provided by Sirtrack, New Zealand. Data included date, time, latitude and longitude, number of satellites and horizontal dilution of precision (HDOP). The HDOP is the likely precision of the location as determined by the satellite geometry, which ranges from 1-100. (Sirtrack GPS Receiver manual, Sirtrack New Zealand). Fixes < HDOP 10 were excluded from the evaluation, because a correct location of the cat could not be assured (Moseby *et al.* 2009).

Home Range

Animals tend to occupy certain areas with greater frequency than others (Dixon and Chapman 1980). This was also apparent in this study and therefore two scales of home ranges activity were used: (1) Minimum Convex Polygon (MCP) using 95% of all fixes closest to the harmonic mean centre. (2) The core area of cats was calculated, using Minimum Convex Polygon employing 50% of all fixes (MCP 50). To calculate MCP 95 and MCP 50, the Home Range Extension tool (HRE tool) for Arc View Geographic Information System (GIS) (Rodgers and Carr 1998) was used.

Despite the fact that cats are predominantly nocturnal, feral cats can also be active during the day (Jones and Coman 1982; Molsher *et al*. 2005). Therefore day and night ranges (MCP 95) were analysed separately to test for potential differences in occupancy. 'Day' was defined from sunrise to sunset (6:35-18:25 hours during the time of study) and differences were tested for significance using a paired t-test.

Overlap in Home Range

Percentage overlaps for each adjacent and overlapping pair of home ranges (MCP 95) were calculated, using the X-tool in Arc

View Geographic Information System (GIS) (Rodgers and Carr 1998).

Activity

The average sum of day-time and night-time movement was calculated and an unpaired t-test was used to analyse differences. The GPS data loggers are only able to record a fix when they have a clear view of the sky. Indication of the cats’ activity pattern can be obtained by analysing the time that the collar transmitter was unable to record a fix, suggesting that the animal may have been in a cave, underground or under thick vegetation, resting or sleeping. Unsuccessful fixes were analysed for each individual and included in the activity evaluation.

Results

Sixteen cats (12 males, 4 females) were collared, one of which (B1) died prior to baiting of unknown causes. Data of this GPS-collar were excluded from evaluation.

Home Range Size

The home range size of 15 collared cats ranged from 2.74 km^2 (MB7) to 26.2 km^2 (MB2), with a core area, an average of 39% of the home range area, ranging from 1.01 km^2 (B2) to 8.5 km^2 (MB2) (Table 1). Home ranges of male cats tended to be larger (MCP 95: 10.7 ± 6.7 km^2; MCP 50: 3.9 km^2, n= 11) than those of females (MCP 95: 7.1 ± 5.98 km^2, MCP 50: 3.26 km^2, n= 4), however no significant difference could be detected (t-test: MCP 95 P = 0.717, MCP 50 P = 0.69). No significant correlation between body mass and home range (R^2 = 0.053; P = 0.408) and core area size (R^2 = 0.122; P = 0.202) was found.

Table 1. Home range and core area size (km^2) of 15 feral cats on Dirk Hartog Island in April 2009.

Cat ID	M_b (kg)	Sex	Data collection (minutes)	MCP 95 (km^2)	MCP 50 (km^2)
DH5	5.1	M	10	3.87	2.09
DH5.1	4.25	M	10	7.15	4.29
DH12	5	M	10	11.1	5.23
DH17	5	M	10	18.54	7.69
DH27	5.1	M	40	11.93	2.46
DH27.2	4.5	M	40	5.95	2.01
DH29	4.75	M	80	12.85	4.58
MB8	5.5	M	10	8.88	1.74
MB2	2.7	M	80	26.22	8.5
MB3	3.2	M	80	7.21	3.25
MB6	4.7	M	80	4.1	1.14
B2	3.5	F	10	3.67	1.01
MB5	2.6	F	10	15.79	8.18
B3	3.7	F	10	6.37	2.18
MB7	3.5	F	80	2.74	1.68
Average				**9.8**	**3.7**

Overlap in Home Range and Core Area

A 49.14 ± 7.01% (mean ± SE) overlap of home ranges (MCP 95) between 18 adjacent and overlapping pairs of cats were detected. Also a 53.6 ± 7.35% (mean ± SE) overlap of the core area (MCP 50) of ten adjacent and overlapping cat pairs was recorded, with three cats MB5, DH 27_2 and DH5 almost completely overlapping with adjacent cats MB6 (96%), DH 27 (84%) and DH5_1 (81%) (Figure 3).

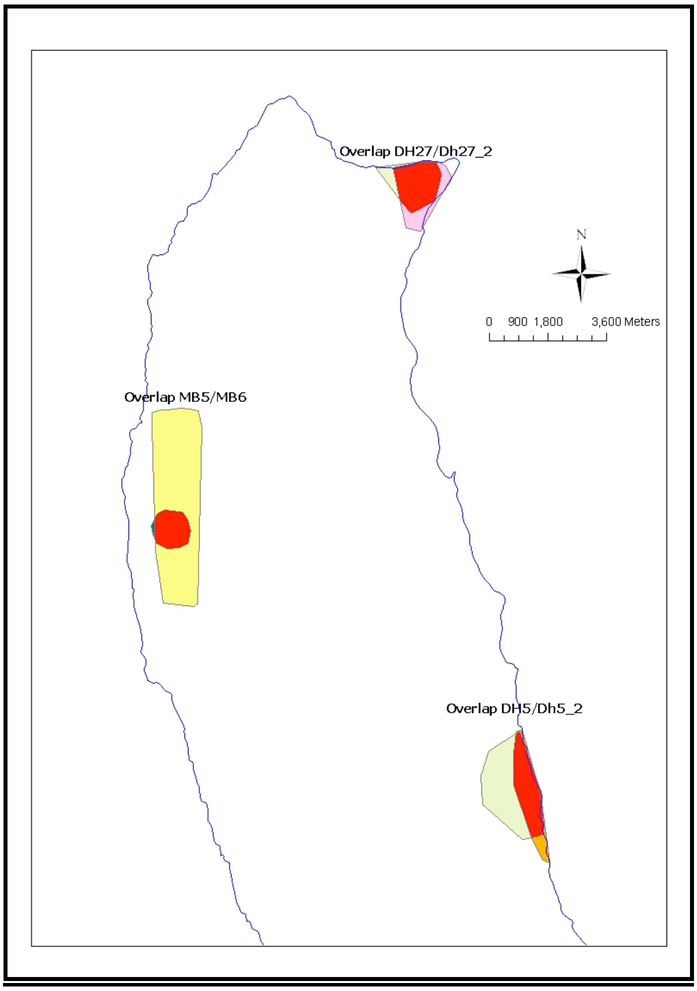

Figure 3. Overlapping core areas (MCP 50, marked in red) of three cat pairs. (MB5/MB6: 96% overlap, DH27/DH27_2: 84% overlap, DH5/ DH5_2: 81% overlap).

Day and Night Ranges

Day ranges (mean: 7.06 km^2) were significantly smaller than night ranges (9.4 km^2, paired t-test: $P < 0.0001$) and overall home ranges (9.76 km^2, $P < 0.0001$), whereas night ranges did not differ from overall home ranges ($P = 0.295$) (Figure 4).

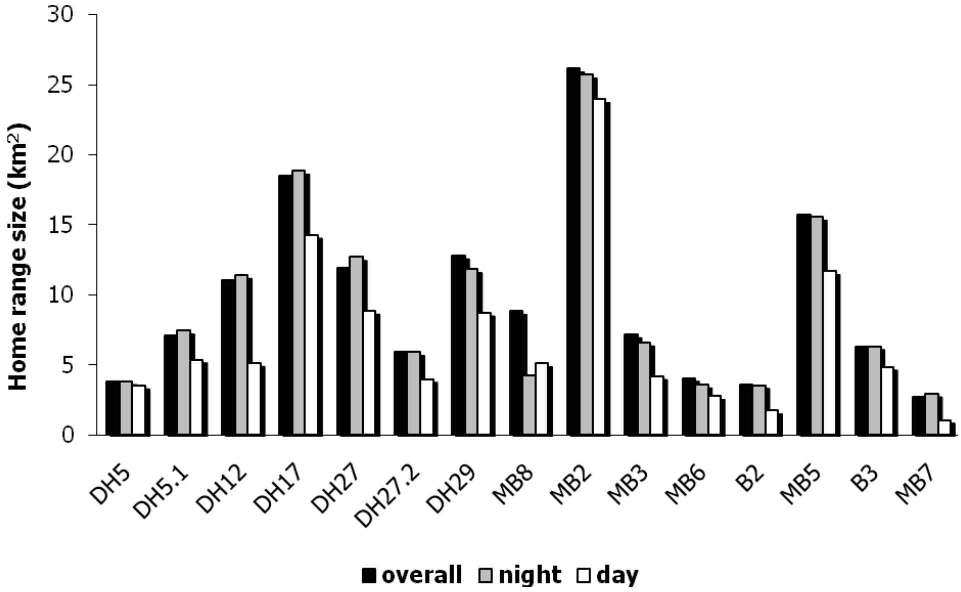

Figure 4. Day, night and overall MCP 95 (km^2) of 15 feral cats from Dirk Hartog Island, in April 2009.

Activity

Distance travelled during the day was 1219 ± 169 m (mean ± SE), which is significantly smaller than during the night (4102 ± 413 m, $P < 0.0001$). A significant difference in recorded fixes was detected, with an average of 68.5 ± 5.9% (mean ± SE) during the day and 88.1 ± 4.5% of fixes, recorded during the night ($P < 0.01$, Figure 5).

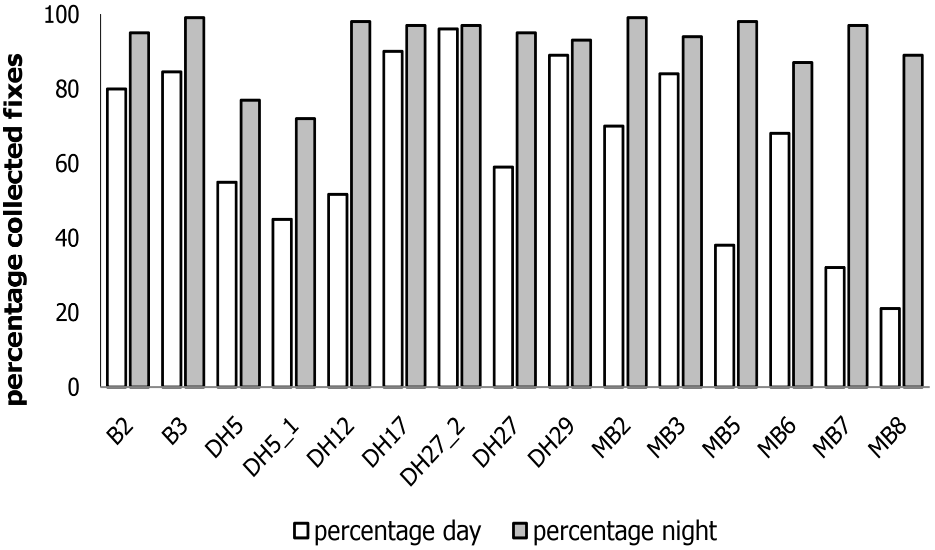

Figure 5. Percentage of collected GPS-fixes during the day (white bars) and night (grey bars) of 15 feral cats.

Discussion

No significant difference in home range size between male and female cats was found, which contrasts with other studies, where female cats were reported to have a smaller home range compared to males (Table 3). However, with the sample size being heavily male biased, a significant difference in home range size might be detectable when increasing the female sample size, especially since there is a clear trend to the females' ranges being smaller. Home range size of the cats in this study were similar to those reported in arid Western Australia (Burrows *et al.* 2003), but smaller than cats from arid rangelands and semi woodlands (see Table 3).

It has widely been reported that home range sizes depend on food availability, and that low prey abundance results in large home ranges in carnivores (Sandell 1989) and particularly in felids (Poole 1995; du Bothma *et al*. 1997; Edwards *et al.* 2001; Burrows *et al*. 2003). Although no study on prey availability was conducted on Dirk Hartog Island, an apparent house mouse (*Mus musculus*) abundance was noted, when this study was carried out, possibly due to significant rainfall events over previous years (Dept. Meteorology rainfall records 2000-2009). In addition, all cats were in very good condition, with noticeable high body fat deposition, which was detected in the course of the surgery for body temperature loggers (iButtons) implantation into eight of the 15 feral cats (Chapter 3). A number of studies (Edwards *et al.* 2001; Burrows *et al.* 2003; Moseby *et al.* 2009) suggest that nutritional stress and/or limited food availability strongly influences the home range and movement patterns of cats. Animals compete for a number of resources, e.g. food, shelter and breeding partners and one way of excluding potential competition from the resources area is showing territorial behaviour (Maher and Lott 1995). Studies on the social structure of feral cats have however shown that cats tolerate each other and that they even built 'feeding groups' on a small Japanese island (Turner and Mertens 1986; Yamane *et al.* 1994). This finding is confined to small islands or urban and farm environments, where cats are stray, possibly still co-dependent on humans. In this study however, a high percentage of home range overlap (49%) was recorded, which suggests that cats probably accepted other individuals in their home range. Moreover, young cats might still establish their home ranges, with MB2 and MB5, the smallest cats, showing big home ranges and overlap of home ranges with five other cats. Similarly, mature, large male cats had a high degree of home range overlap, with DH5 (5.1 kg) sharing 72% of his home range with DH5_1 (4.25 kg), and a core area overlap of 81%. In general, a high percentage of core area overlap was recorded for three cats, having almost their complete core area in other cats´ core areas. This finding is not consistent with the study of Molsher *et al.* (2005), where cats in central west New South Wales showed a high degree of overlap in home ranges (21%), but more separate core areas (7%). This suggests that cats in this study have a high degree of interaction, possibly due to the high prey abundance and therefore less competition pressure.

Daily ranges were significantly smaller than the night ranges, suggesting that cats were less active during the day. This is supported by the significantly lower percentage of fixes collected via the GPS-collar during the day, possibly due to cats sheltering under bushes, underground or in caves. Cats on the west coast of the island (consisting of high cliffs and cave systems), show a lower percentage of positive fixes during the day (MB 5-8), which might be due to resting in caves. Cats on the east coast and in the middle of the island did not have caves accessible for shelter, and therefore relied on bushes and burrows, where the GPS-collar might still have been able to collect a position fix. However, no significant difference in percentage fixes between these cat groups was detected. Also, the activity of cats indicated a more nocturnal behaviour, with a significantly greater distance travelled during the night time, compared to day time. Only two other studies on day and night ranges of feral cats are available (Langham and Porter 1991; Molsher *et al.* 2005), with Langham and Porter agreeing with the finding of this study, showing that both male and female cats occupying a larger range during the night in spring and summer. Molsher *et al.* (2005), in contrast, did not find a difference in range occupancy between day and night. Both studies suggest that accurate tree cover during the day, or respectively cooler days, would allow daytime activity (as shown from Molsher *et al.* 2005). Their findings agree with this study, with vegetation on Dirk Hartog Island being sparse, with small bushes, varanid burrows and caves being the only shelter during the day. Nevertheless, mild spring temperatures during the study possibly still allowed cats to be active during day time, with an average of 1219 m travelled during the day, which might change with season.

Detailed knowledge from this study regarding home range sizes and patterns will enable the design of control programs to be planned on a sounder scientific basis than previously. Such information will assist in the planning of flight transect widths to maximize the likelihood of feral cats encountering a bait within the shortest possible time following a baiting program. This will optimize baiting efficacy and provide a more cost-effective baiting campaign. Feral cat track activity at plots along survey transects, usually along existing tracks, is used to monitor cat abundance before and after baiting programs. This information is then used to determine the impact of the baiting program. In situations where eradication of feral cats is required, such as islands, surveys are undertaken to locate cats that have survived the baiting program so that they may be removed. These surveys are conducted along cross-country transects as track networks are usually limited. To be able to detect these animals within the survey period it is critical to successfully eradicating cats as soon as possible. Further analysis of the movement data will enable rates of encounter (detection probabilities) to be determined for cross-country survey transects, at various widths across the island. It will then be possible to select the best spacing for these transects to optimize encounter during survey periods.

Table 3. Comparison of home range sizes of male and female cats on mainland Australia and Islands. All home range sizes were calculated, using minimum convex polygon methods (MCP 100) and therefore this study calculated MCP 100 for the comparison with literature values.

Location	**Landscape**	**Mean range size (km^2)**		**No of cats**		**Reference**
		male	female	male	female	
Western Australia	open bushland	11.2	7.2	11	4	this study
South Australia	arid rangelands	32.32	20.78	7	3	Moseby *et al.* 2009
Northern Territory	semi woodlands	22.1	-	4	-	Edwards *et al.* 2001
Western Australia	arid desert	13.5	7	2	1	Burrows *et al.* 2003
Victoria	semi-arid	6.2	1.7	4	2	Jones & Coman 1982
New South Wales	open woodland	4.23	2.38	11	4	Molsher *et al.* 2005
Tasmania	open forest	1.54	0.29	2	1	Schwarz 1995

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Conclusions

The study presented in this thesis aimed to improve the understanding of ecophysiological adaptations of feral cats in Australia. Feral cats are responsible for the decline and extinction of a number of native species and the failure of a number of reintroduction attempts, especially in the Australian arid zone. Understanding the cat's physiology and ecology in terms of its environmental adaptations to different climates, seasons and captivity could increase the understanding of the cat successful colonisation of the Australian continent. Furthermore this information might point to vulnerabilities that could be used, for further refinements in the strategies and methods to control cats.

This study focused on the energetic and ecophysiological aspects of feral cat biology, in particular metabolism, body mass, body temperature patterns and home range size. I employed methods that facilitated the measurement of these parameters in the field to obtain data most closely representing feral cats in their natural physiological state, without the effects of captivity (as shown in Chapter 4). Data obtained by measuring basal metabolic rates (BMR) of feral cats on the same day of capture gave the best possible insight into the energetics of feral cats under natural conditions. The use of implanted body temperature data loggers (iButtons) in free-ranging feral cats improved the understanding of body temperature (T_b) patterns under natural conditions. Global Positioning System (GPS) technology allowed the study of movement and activity patterns as well as home ranges and interaction of feral cats on a semi-arid island off Western Australia.

At the commencement of this study, it was hypothesized that feral cats could adapt to challenging environmental conditions (e.g. arid zone) by a possible decrease in BMR and M_b (body mass). The study however did not find a difference in BMR between feral cats from arid, temperate and tropic climate zones (Chapter 1 and 2), or compared to a same-sized Felidae (Chapter 5). Animals used in this study were all in very good condition, without any signs of malnourishment or starvation. It is possible that starving or malnourished individuals might exhibit a decrease in their BMR as consequence of low prey availability rather than climate.

The M_b analysis in Chapter 2 showed that cats from tropical and temperate islands had a smaller M_b compared to cats from a semi-arid island population and three mainland populations. This difference in M_b was possibly be due to inadequate levels of certain nutrients in their diets at least for the tropical island cats, rather than due to climate (e.g. Bergmann’s rule) or isolation (e.g. Island rule).

While my data did not show a reduced BMR of cats from arid conditions, they did indicate a 25% lower BMR of cats in summer compared to winter measurements, thus a marked seasonal effect. This was possibly due to seasonal changes of food availability (reptiles and insects are mostly inactive during the winter) and breeding activity. Feral cats may respond to these seasonal changes by increasing home range sizes to obtain daily food requirements and to find breeding partners. The decrease in BMR in summer could also be due to lower metabolic heat production and therefore body temperature.

Examination of T_b patterns of free-ranging feral cats showed regularly high T_b peaks of over 40 ^{0}C, which likely reflect a time of hunting or high activity (e.g. territorial fight) (Chapter 3 and 4). This high tolerance to temperature extremes, might allow the cat to exploit a broad temporal niche and a broad range of prey species as food items. The activity patterns of cats in this study did show a predominantly nocturnal behaviour (Chapters 3, 4 and 6), thereby conserving water and reducing the potential for heat stress by avoiding the daytime heat. This nocturnal behaviour however is possibly flexible with season and ambient conditions.

The study of home range and movement patterns of feral cats on a semi-arid coastal island (Chapter 6), demonstrated for the first time that core areas of several cats may overlap by more than 50%. This is possibly due to high prey abundance resulting in reduced territorial pressure. These physiological aspects and behavioural flexibility found in this study may explain the cats' successful colonisation of the entire continent and specifically the arid zone.

The second part of my thesis aimed to quantify the effect of captivity on two physiological parameters: BMR and T_b-patterns (Chapter 4). A 36% decrease in BMR was detected for cats held in captivity for a period of one year. These metabolic adjustments to captivity are most likely driven by a number of differences between the natural and captive environment, including availability and quality of food, activity levels, and associated changes in body composition. During the course of captivity, the cat's T_b rhythmicity changed from nocturnal (as found in free-ranging cats) to a diurnal tendency with a less pronounced day-night rhythm. In captivity, many changes occur in the various factors likely to influence the natural T_b pattern, such as interaction with competitors, social behaviour and food availability. On the other hand, new potential influencing factors are introduced, including a daily feeding regime at midday and a restricted activity and exercise area. Results of this study certainly show that feral cats are effected by changing conditions (e.g. captivity) and that characteristics of physiological parameters of free-ranging cats should not be inferred from data derived from captive individuals, further discussed in Chapter 5.

Even though no physiological adaptations in BMR and M_b to challenging conditions (here aridity) were detected, the changes caused by captivity demonstrate the flexibility in cats' physiology. It may be possible that feral cats are able to adjust physiological parameters to adapt to changing conditions. This study might not have been able to detect these adjustments (such as a decrease of BMR in the arid zone) since the feral cats that were measured may not have been physiologically challenged in their environment. I believe that a combination of behaviour (e.g. nocturnal behaviour, opportunistic hunting) and physiological traits (e.g. tolerance of high T_b, direct physiological change to varying conditions) allowed the feral cat to colonize Australia's versatile climate zone.

This study is the first to present data of physiological parameters on entirely free-ranging, undisturbed cats. It has improved the understanding of cats' physiological flexibility to season and captivity and may also have implications for the management of the feral cat problem in Australia. In the arid and semi-arid zone of Western Australia, aerial baiting occurs in late autumn to early winter since this is the time that prey abundance is usually at its lowest. The feral cat bait (*Eradicat®*) contains 4.5 mg of the toxin sodium monofluoroacetate (or compound 1080) per bait and this is more than sufficient to kill feral cats in the upper weight range. The 25% increase in BMR recorded in cats in winter compared to summer, shown in this study, may result in an increase in bait uptake and the toxin being more readily absorbed into the cat's metabolism at this time of the year. However, if baits are presented during the summer months when BMR is reduced then the slower rate at which the toxin is taken up by the cat's metabolic processes may allow more of the toxin to be neutralised. If the dosage of 1080 is reduced from 4.5 mg to 3.0 mg, as happened with baits used for fox control in Western Australia, then this may result in reduced toxicity of baits considering the cat's relatively higher 1080 tolerance and changes in BMR. This may have further consequences in that not only will there be a reduced mortality of cats that consume baits but cats may consequently develop bait shyness therefore leading to reduced bait uptake and an overall reduction in baiting efficacy.

Curriculum vitae

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Career

1998	Abitur (graduation of grammar school), Grade: 3.1
1998 - 1999	Language-school in Sydney (Cambridge degree), Australia, as well as volunteer work in Australia
04 - 08. 2000	Biological preparation course in Cologne
2000 - 2002	Basic studies in biology at the Johann Wolfgang Goethe-University, Frankfurt
2002	Intermediate diploma, Grade: 2.1
07- 08. 2003	Study Trip to Shark Bay, Western Australia in cooperation with the Dept. of Environment and Conservation (DEC)
2002 - 2004	Main study periods with following subjects: • Neurobiology • Animal physiology • Toxicology

04. 2004 - 07. 2005	Assistant work at the Johann Wolfgang Goethe-University
10. 2004 - 04. 2005	Field study in Western Australia, diploma thesis: “*Energy consumption and thermoregulation of Australian marsupials and their exotic predators: the feral cat*”.
04- 08. 2005	Co-Supervisor of a preparation seminar prior to a study excursion in August 2005 to Perth, Western Australia, including presentations about Australian wildlife, environmental problems as well as teaching how to write ethic applications for animal experiments.
07. 2005	Diploma degree, Grade: 1.1
08– 10. 2005	Supervisor in Perth, Western Australia for a German student group in cooperation with the Dept. of Environment and Conservation and the Johann Wolfgang Goethe-University, Frankfurt Germany. Work included measuring metabolic rates of feral cats and imparts the background of the importance of this project.
10. 2005 - 03. 2009	Experimental work for PhD project: `*Ecophysiology of feral cats (Felis catus) in Australia*`, including field trips to several study sites in Western Australia and Victoria; Literature research and Supervision of student groups.
03– 12. 2009	completion of PhD thesis.

Publication list

- **2005**

Hilmer S. (2005): Energiehaushalt und Thermoregulation australischer Beuteltiere und ihrer exotischen Prädatoren: die verwilderte Hauskatze. Diplomarbeit J.W.Goethe-Universität Frankfurt am Main.

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- **2007**

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- **2009**

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