COMPARATIVE ASPECTS OF THE THERMAL BIOLOGY OF AFRICAN & AUSTRALIAN PARROTS

by

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"Ecology is nice, behaviour is good, but first you have to know the anatomy and physiology."

HORST SCHWASSMANN

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg from February 2004 to December 2005, under the supervision of Professor Mike R. Perrin and Professor Colleen T. Downs.

This dissertation, submitted for the degree of Master of Science in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

S.L. BURTON
December 2006

I certify that the above statement is correct

M. R. Perrin

PROFESSOR M.R. PERRIN
Supervisor

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To my PARENTS, your sacrifices have made it possible for this dream of mine to become a reality. You have believed in me and guided me throughout my life, while affording me the opportunity to live my life in the outdoors. Your belief in me, and support of everything I have done, has meant the world to me, thank you.

To my wife CURSTY, your love, support and patience have come without question, especially through the last few months. You have anchored me.

ABSTRACT

Deserticolous birds inhabit an environment characterised by high ambient temperatures and low rainfall that has low primary productivity. The combination of these factors may lead to the evolution of adaptations that minimise food and water requirements. One physiological adaptation that has been found in many deserticolous birds is the reduction of basal metabolic rate (BMR).

I measured metabolic rate in the laboratory using four species of African lovebirds (*Agapornis*), and four species of Australian grass parakeets (one *Neopsephotus* and three *Neophema*), all similar in body mass. Tests for differences between groups were carried out using both conventional and phylogenetically independent methods. The BMRs of the lovebird and grass parakeet species were not statistically correlated with habitat type. These results confirm the findings of previous studies on the effect of desert conditions on the BMR of parrots. I also found no significant differences in BMR between the species assemblages from different continents. The lack of significant differences in BMR between deserticolous and non-deserticolous parrots supports the idea that birds are "ex-adapted" to living in desert environments. I suggest that the results may have been affected by phenotypic plasticity in BMR, as recent evidence has shown that the scaling exponent of BMR differs between captive-raised and wild-caught birds.

To elucidate the effect of origin (captive-raised vs. wild-caught) on the BMR of birds used in this study a large scale analysis of bird BMR data was undertaken. BMR and body mass data for 242 species of birds were obtained from the literature, this study, and unpublished data from various sources. A phylogeny was constructed using molecular and morphological phylogenies from the literature, and analysed using conventional and phylogenetically independent methods. The conventional analysis found significant differences in the scaling exponents of BMR of captive-raised and wild-caught birds. However the phylogenetically independent method showed non-significant differences between these two groups. Conventional analysis of differences between parrots and all other birds yielded significant differences between these two groups, with parrots having significantly higher BMRs than other birds. Again the phylogenetically independent analysis found non-significant differences between these

two groups. A test of homogeneity of variance between these two groups found significant differences between the variances of the two groups, probably due to disparity in sample size and range of body sizes. The conventional and phylogenetically independent tests for differences between captive-raised and wild-caught parrots yielded non-significant results, suggesting that the parrots are not subject to the phenotypic adjustments postulated for all other birds.

The lack of significant differences between captive-raised and wild-caught parrots suggests that the analyses of differing habitat type for African and Australian parrots is indeed valid.

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CHAPTER ONE

DESERTS AND PARROTS: HOW WELL ADAPTED ARE DESERT DWELLING PARROTS TO THEIR HABITAT?

DESERTS AND BIRDS

The Protean Concept of Deserts

The definition and delimitation of deserts is a fluid and highly debated concept. Over the centuries deserts have been classified and delimited in numerous different ways (Noy-Meir 1973; McGinnies 1979; Shmida 1985). Some authors have delimited desert boundaries purely on the basis of precipitation (Noy-Meir 1973; Shmida 1985), while others have incorporated the many other criteria that may be used to delineate deserts, in conjunction with precipitation, to generate a more holistic perspective (Thornthwaite 1948). In this study, we will make use of the classification system that Meigs (1953) developed using Thornwaite's (1948) index of moisture availability (I_m). I_m is an index derived from data on precipitation, the maximum ambient air temperature (T_a) of the hottest month of the year, and the minimum T_a of the coldest month of the year (Thornthwaite 1948). Meigs (1953) used these I_m values to classify the worlds' deserts into semi-arid, arid, and hyper-arid. In addition a desert could only be considered hyper-arid if there was at least one recorded occurrence of 12 consecutive months without precipitation (Meigs 1953).

Using Meig's (1953) classification 36.3% (52.9 of 149 million km^2) of the earths' land surface is semi-arid, arid, or hyper-arid. All of the areas he identified fall under the catholic term "desert", however, deserts on the different continents have very different histories, geomorphologies, ambient temperature ranges, and levels of aridity (Thornthwaite 1948). These factors influence the availability of food and water resources and the thermoregulatory demands that are of importance for the survival of the resident bird species (Thornthwaite 1948; Tieleman & Williams 2000).

Desert-Dwelling Birds

Deserts are broadly characterised by high temperatures and low rainfall. These factors combine to produce environments that have low primary productivity and little or no standing water (Tieleman et al. 2003). Deserts therefore represent some of the harshest habitats on earth, and present numerous challenges for the animals and plants that live in them (Fisher et al. 1972). Many desert dwelling organisms have been recorded as having structural or physiological adaptations to counter the harsh conditions of extreme heat and lack of water (Gibbs 2002). However, birds have long been thought to have no physiological or structural adaptations to deserts (Bartholomew & Cade 1963; Maclean 1996). Maclean (1996) stated: "*what seems to be adaptive in birds to the desert environment is in fact intrinsic to the avian condition*". Maclean (1996) and Bartholomew and Cade (1963) therefore argued that birds are in essence ex-adapted to survive the added pressures that desert environments place on their energy and water budgets. Recent work has, however, challenged this standpoint (Tieleman & Williams 2000) (For a full review of these ideas see Energy and Water in Deserts, pg. 5).

Many desert-dwelling birds have employed non-physiological means of dealing with the hot and dry conditions that occur in these extreme habitats. Behavioural adaptations enable birds to avoid the high summer air temperatures and associated evaporative cooling costs. Thus, many desert-dwelling birds reduce or suspend activity during the hottest hours of the day (Ricklefs & Hainsworth 1968; Austin 1976; Austin 1978; Wolf & Walsberg 1996; Wolf et al. 1996; Wolf 2000). For example, at environmental T_a above 35°C, the Cactus Wren (*Campylorhynchus brunneicapillus*) significantly reduces the number of visits to the nest, favours shaded areas and reduces overall activity (Ricklefs & Hainsworth 1968). Verdins (*Auriparus flaviceps*) also reduce their activity levels with increasing ambient temperatures (Austin 1976; 1978). Below T_a = 35°C the Verdin spends as much as 75% of each hour foraging, but at T_a = 45°C or more foraging activity is reduced to just 25% of each hour (Austin 1976; 1978). Almost all reductions in activity levels are accompanied by movement from sunlit to shaded areas (Austin 1976).

There is also evidence that birds living in deserts choose very specific microhabitats as thermal refuges (Wolf 2000). These thermal refugia reduce the thermal load and evaporative moisture loss of the birds that make use of them (Wolf 2000). In a classical example of this behaviour, four species of lark were recorded making use of the burrows of Egyptian spiny-tailed lizards (*Uromastyx aegypticus*) in the Arabian Desert (Williams et al. 1999). One of these species, the Hoopoe Lark (*Alaemon alaudipes*), was recorded using burrows that had a T_a of 41.5°C, while the external T_a was 44.1°C (Williams et al. 1999). Williams et al. (1999) estimated that occupying the burrow reduced the birds daily water loss by 65 - 81%.

Reduction in activity, combined with the choice of specific thermal refugia helps desert-dwelling birds to minimise water losses during the hottest part of the day (Wolf 2000). If the birds remained active they would accrue a water deficit for two reasons. Namely, first, the production of metabolic heat through activity, which necessitates an increase in evaporative cooling so as to maintain body temperature (Wolf 2000). Second, there would be more water lost to evaporative cooling in sunlit foraging areas than in the shaded thermal refugia occupied during the suspension of activity (Wolf 2000). This is caused by the increased T_a associated with sunlit foraging patches (Wolf 2000).

Desert-dwelling birds also possess one characteristic that sets them apart from most other deserticolous endotherms, they can fly. The ability to fly affords birds living in deserts a means of escape from extreme high T_as, as well as during periods of low resource availability, or to make use of an ephemeral resource (Wolf et al. 2002). Wolf et al. (2002) state that White-winged Doves (*Zenaida asiatica*) and Mourning Doves (*Zenaida macroura*) inhabit the Sonoran Desert only during the summer breeding season, and winter in Mexico or Central America. They draw attention to the fact that the White-winged Doves make use of saguaro cactus (*Carnegeia gigantea*) during its flowering and fruiting season, and suggest that the cactus is an important food source for the doves during their breeding season. The doves are using the Sonoran Desert for breeding because of a resource that is unavailable in the deserts where they over-winter. The White-winged Doves ability to fly allows it to exploit resources in various deserts, and so optimise its breeding success. Extreme conditions can also be avoided – negating selection pressure for physiological adaptations.

Threats to Desert Dwelling Birds

The largest threat to the continued survival of deserticolous bird populations is not habitat loss, as is the case for forest dwelling species, but rather the increase in air temperatures that is associated with global warming (Wolf 2000). Air temperature fluctuations have occurred previously, on a global scale, and the numerous hot and cold periods in our past are easily detectable in the ice cores of the polar caps (Broecker 1975). However, the rate at which air temperatures are rising at present is much faster than at any time in recent history. This increased rate of air temperature warming, commonly referred to as global warming, is thought to be associated with increased burning of fossil fuels that started at the beginning of the industrial revolution (Broecker 1975). The greenhouse gases that are emitted when fossil fuels are burnt act to trap heat within the atmosphere, thus upsetting the natural release of excess heat into space (Broecker 1975). Also associated with the industrialisation is the release of CFCs into the atmosphere which has caused holes in the ozone layer and increased levels of solar radiation reaching the planet's surface. The combination of these events has the effect of raising global temperatures. Previous rapid temperature increases of the sort that we are experiencing now have taken place in the past, but usually over 10 – 20 thousand years (Wing et al. 2005). Current temperature increases, and those predicted for the future, are taking place in 100 – 200 years (IPCC 2001). The previous global warming event at the Paleocene-Eocene boundary, although slower acting, caused large scale changes in faunal and floral assemblages (Wing et al. 2005).

Best estimates indicate that global temperatures will increase by 1.4 - 5.8° C by the year 2100 (IPCC 2001). The implications of such an increase in temperature is that desert dwelling species may start to shift their range or die as the temperatures rises (Wolf 2000). An example of this would be the predicted response of the Verdin, a small bird (ca. 6.5g) that is resident in the Sonoran Desert year round, where the temperature can exceed 42° C for 8 or more hours per day (Wolf & Walsberg 1996). Between T_a = 38 - 48°C this little bird's evaporative water loss increases seven-fold, and may account for as much as 5% of the birds body mass being lost per hour (Wolf & Walsberg 1996). An increase of 1.4 - 5.8°C would mean that this species' ability to maintain an adequate state of hydration would be compromised (Webster 1991; Wolf & Walsberg 1996). Many species living in deserts are prone to such pressures, and global warming may drive these species to the edge of extinction, or cause shifts in the distributions of species out of the deserts. Global warming is already affecting the timing of leaf and flower development in all geographic regions (Root et al. 2003; Cotton 2003; Parmesan & Yohe 2003; Wing et al. 2005), as well as the migratory routes of birds, the timing of breeding, and the use of hibernation in some species (Inouye et al. 2000; Peñuelas & Filella 2001; Cotton 2003; Sanz et al. 2003).

ENERGY AND WATER IN DESERTS

Basal and Field Metabolic Rate

Generally, birds have high rates of mass-specific metabolism, and desert birds face the challenge of balancing their energy budgets while living in an environment with low primary productivity. The evolution of mechanisms to reduce the energy expenditure of desert birds, and therefore enable them to survive with the low resource availability, have been proposed by several authors (Dawson & Bennett 1973; Schleucher et al. 1991). Any physiological mechanism that reduces energy expenditure in free-living birds should be mirrored in lower basal metabolic rates (BMR). The idea that desert birds have reduced BMRs has been proposed by several authors (Dawson & Bennett 1973; Weathers 1979; Withers & Williams 1990; Schleucher et al. 1991), however, a quantitative comparison between desert and non-desert birds was only recently performed by Tieleman and Williams (2000). Tieleman and Williams (2000) used both least squared regression (LSR) and regressions using phylogenetically Independent Contrasts (PIC) to test whether the BMR of 21 arid and 61 mesic bird species, from a wide range of geographic origins, differed. The desert species have BMRs that are ~17% less than the non-desert species. The underlying physiological mechanism that causes this reduction in the BMR of desert birds may be due to a smaller quantity of metabolically active tissues. The heart, liver and kidneys may be smaller, as it has been shown that these organs contribute a disproportionately large amount towards BMR when compared with other tissues (Konarzewski & Diamond 1995; Piersma et al. 1996). However, the underlying cause, whether phenotypic responses or adaptations to the environment, remain unresolved.

Basal metabolic rate is measured under controlled laboratory conditions (McKechnie & Wolf 2004), while field metabolic rate is measured using doubly labelled water (Nagy 1987; Nagy et al. 1999; Anava et al. 2000; Kam et al. 2003). The difference between desert and non-desert bird BMRs (Tieleman & Williams 2000) gains significance if field metabolic rate (FMR) shows the same relationship. Nagy (1987) performed an analysis to determine whether FMR differed between desert and non-desert birds, and found that desert birds had FMRs that were 50% lower than non-desert birds. More recently, Tieleman and Williams (2000) performed the same analysis with a much larger sample size and found that the FMR of desert species was 49% lower than that of non-desert species. It allows desert birds to survive in extreme environments, and adds weight to the argument that reduced BMR is the one of the physiological mechanisms by which this reduction is achieved.

Water Flux

Most birds living in deserts have to maintain a state of hydration in an environment that is hot and desiccating. Many of these birds obtain the water from the food they eat, and the water released during catabolism of energy substrates. Some species can survive on seed that has as little as 15% water (Maclean 1996). The species that can survive on dry food sources tend to be found almost exclusively in deserts, suggesting that this trait is under strong selection in desert environments. Many desert birds dehydrate before high ambient temperatures and high levels of solar radiation force them into the shade (Williams et al. 1995), or when water sources are too far from feeding areas. In these situations some birds tolerate losses of as much as 35% of body mass (Dawson et al. 1979).

To interpret avian water budgets, it is helpful to understand how well metabolic water production can replenish the losses incurred by the body water pool caused by evaporation (MacMillen 1990; Williams 1999). When millet seed is catabolised it yields 0.62mg of water per millilitre of oxygen consumed (Schmidt-Nielsen 1984). This may seem insignificant, but Williams (1999) shows that at $T_a \leq 20°C$ Dune Larks produce more metabolic water than is lost through evaporation. They produce excess water during cool nights and use this water to counter losses associated with high ambient temperatures during the day (Williams 1999).

Field water flux rates of desert birds are lower than those of non-desert birds (Nagy & Peterson 1988). However, Tieleman and Williams's (2000) analysis of a larger sample showed no significant differences between desert and non-desert species. Therefore, results should be interpreted with caution. The fact that birds resident outside of deserts might have higher rates of water flux than birds inhabiting desert environments does not mean that desert birds are better at conserving water. This difference may be explained by the fact that birds outside of deserts have direct access to free-standing water, and can drink more water than is necessary to maintain water balance, thus over-inflating the values for non-desert species. This could lead to the erroneous conclusion that desert birds are exhibiting an adaptive strategy to deal with their harsh environment.

PARROTS

Desert Parrots

Parrots, including lories, lorikeets, parakeets, cockatoos, lovebirds and macaws, comprise the order Psittaciformes. The family Psittacidae excludes the lories and lorikeets, but may include or exclude the cockatoos (Forshaw 1977; Collar 1997; Juniper & Parr 1998; Forshaw 2002). All parrots are characterised by zygodactylous feet, a fleshy cere, and a unique bill structure and shape (Collar 1997; Juniper & Parr 1998). The zygodactylous feet may indicate that the parrots evolved in forested areas, as an arboreal adaptation for climbing and grasping (vegetation and food), and most parrot species live and breed in the tropical and subtropical forests of the world (Forshaw 1977; Collar 1997; Juniper & Parr 1998; Forshaw 2002). Some species, especially in the Old World, have, however, left the forest and now inhabit open woodlands, grasslands and the semi-arid and arid environments of Australia and Africa (Juniper & Parr 1998). Most parrots, including species living in open woodland, are inextricably tied to trees for breeding, and most of them breed only in tree cavities (Eberhard 2002; Downs & Symes 2004).

Being primarily forest species means that parrots have evolved to make use of various forest plant parts, namely fruits, blossoms, nectar, pollen, leaves, buds, and even occasionally the bark (Juniper & Parr 1998). Parrots living in open woodland, and areas with few or no trees, have tended to become granivorous (Homberger 1994). Parrots inhabiting semi-arid, arid and hyper-arid environments are faced with the same physiological challenges as all other desert birds, but they may have the added disadvantage of being primarily adapted for living in forests. If parrots are indeed able to survive with the extremes of temperature and water deprivation that are prevalent in deserts, then they have either adapted to these environments using the physiological and behavioural mechanisms listed above, or they add weight to Maclean's (1996) idea that birds are indeed intrinsically adapted to cope with desert environments.

Much of the research into parrots has focused on their intelligence (Cruickshank et al. 1993; Farabaugh & Dooling 1996), or on their ecology/ conservation biology (Christian et al. 1996a; Bonadie & Bacon 2000). However, there has been some research that has focused on the physiology of parrots (Dawson 1965; Lindgren 1973; Bucher 1981; Bucher 1983; Weaver 1987; Bucher & Morgan 1989; Williams et al. 1991). The physiological work is often of a focused nature, and in many cases the methods employed are dated. This study therefore aims to examine whether desert-dwelling parrots are adapted to their harsh environments by comparing desert-dwelling species with non-desert-dwelling species that are closely related. I tested the idea that desert-dwelling parrots have lower BMRs than non-desert-dwelling parrots, and that desert-dwelling parrots have lower water fluxes than non-desert-dwelling parrots. This study is laboratory based to remove the effects of environment, and to provide stable conditions that simulate a common-garden experiment (Wikelski et al. 2003).

Threats to Parrots

Throughout their range parrots are under threat, primarily because of international trade for their beautiful plumage and the destruction of their habitat (Low 1984; Evans 1991; Christian 1993; Marsden & Jones 1997; Wright et al. 2001; Perrin 2002; Downs & Symes 2004). Parrots are traded in large numbers because of their bright, colourful plumage, and value as exotic pets (Gonzalez 2003). Many parrots are removed from the wild as chicks having been poached from nests, and the mortality rate of these young birds is exceptionally high (Lambert 1993; Gleuck 1994; Stoltz 1994; Wright et al. 2001). Trade, in association with the destruction of natural habitat, is reducing the populations of many parrots, and some species are recently extinct, or are on the verge of extinction (Prozesky 1978; Low 1984; Joseph 1988; Gnam & Burchsted 1990; Christian 1993; Robinson 1996; Christian et al. 1996a; Christian et al. 1996b; Silvius 1997; Snyder et al. 2000).

With the rapid decline in parrot numbers, many organisations have invested considerable funds in the conservation of parrots. The guarding of nests has taken place (Lindsey 1992), as well as extensive reintroduction programmes from captive breeding stations (Sanz & Grajal 1998; Brightsmith et al. 2004). The use of nest boxes to supplement natural breeding cavities is producing some degree of success (Millam et al. 1988; Moller 1992; Beissinger et al. 1998; Eberhard 2002). However, ideally and primarily the parrots need habitat preservation and protection from poaching, which only comes with the protection of large tracts of land in pristine condition. These habitats are becoming harder to find in this age of expanding human populations, and the consequent need for land and other natural resources. The future of the parrots of the world lies in the education of the people that live in close proximity to them and often become the poachers that deplete wild populations. However those driving the trade, the dealers, are the main cause of the problem. Without this awareness amongst the populations within the parrots range, no conservation effort will be successful.

STUDY SPECIES

African Lovebirds

Four species of small, easily maintained and inexpensive African lovebirds (*Agapornis*) were selected for this study as they were readily available and represent species from an aridity gradient with one species inhabiting mesic areas, two species semi-arid areas, and one in arid areas. All species were classified as semi-arid, arid or mesic by Meigs (1953) classification of deserts.

Agapornis fischeri

The Fischer's Lovebird (Figure 1.1) inhabits *Acacia*-dominated wooded grasslands in Tanzania (Figure 1.2). Their diet is composed primarily of grass and *Acacia* seeds and the species is recorded as drinking daily (Collar 1997). This species is distributed in a semi-arid environment (Meigs 1953).

Figure 1.1. Fischer's Lovebird (*Agapornis fischeri*)

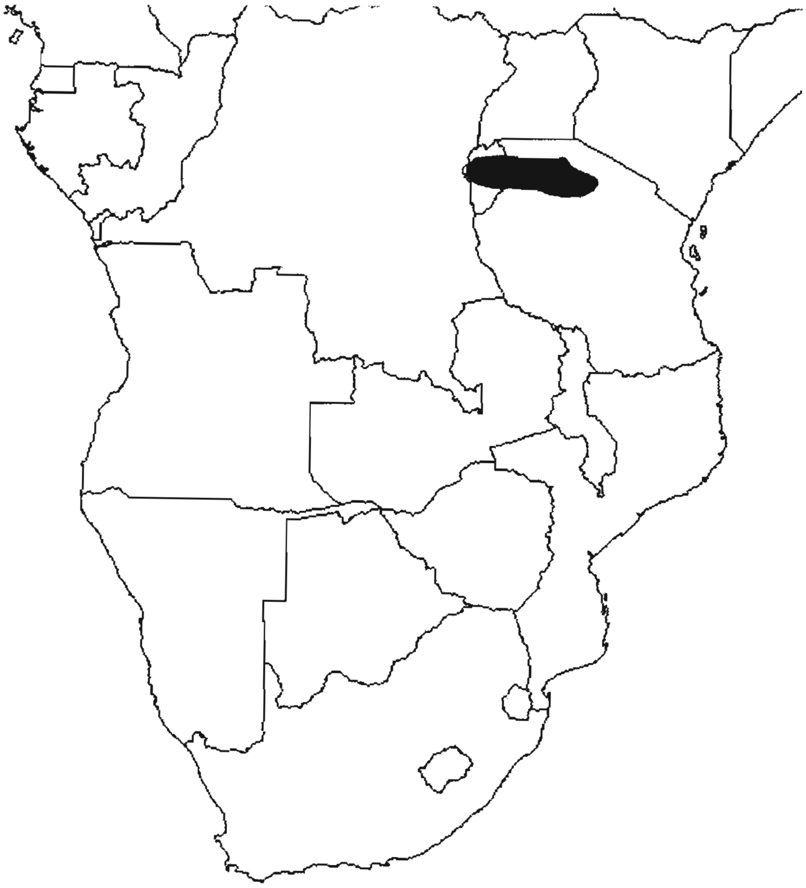


Figure 1.2. Distribution of *Agapornis fischeri* in Africa, after Juniper and Parr (1998)

Agapornis personatus

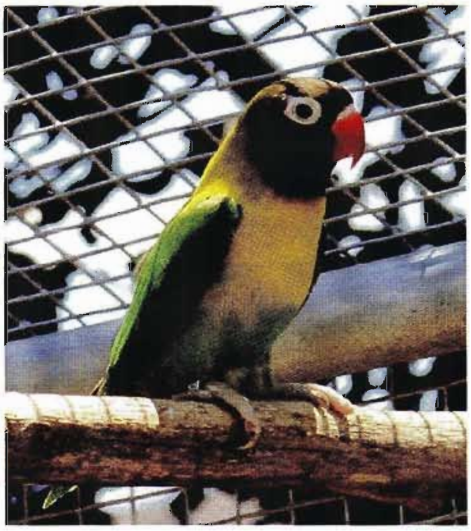


Figure 1.3. **Yellow-collared Lovebird (*Agapornis personatus*)**

The Yellow-collared Lovebird (Figure 1.3) inhabits well-wooded bushland that is dominated by *Acacia*. It is distributed through Eastern Tanzania, and its range overlaps slightly with *Agapornis fischeri* (Figure 1.4). The diet is poorly known, but the birds have been seen eating grass seeds (Collar 1997). This species is distributed in a semi-arid environment (Meigs 1953).

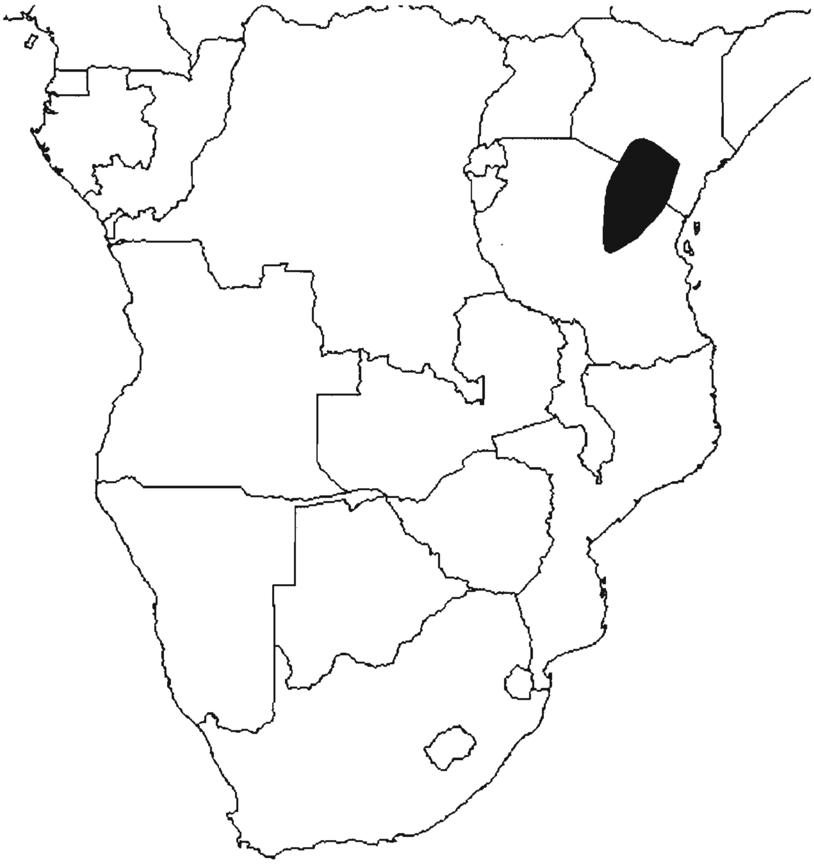


Figure 1.4. **Distribution of *Agapornis personatus* in Africa, after Juniper and Parr (1998)**

Agapornis nigrigenis

The Black-cheeked Lovebird (Figure 1.5) inhabits medium-altitude deciduous woodland dominated by *Colophospermum mopane*. It is distributed through southern Zambia (Figure 1.6). Diet consists mainly of grass seeds, with occasional consumption of other plant parts (Collar 1997). This species is distributed in a mesic environment (Meigs 1953).

Figure 1.5. Black-cheeked Lovebird (*Agapornis nigrigenis*)

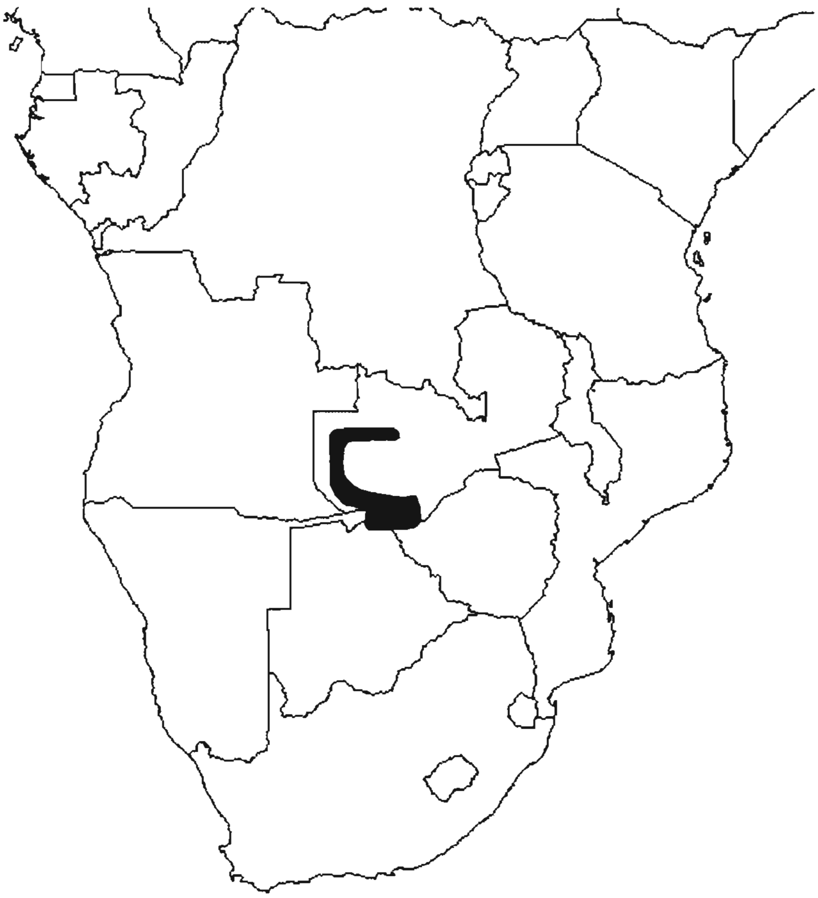
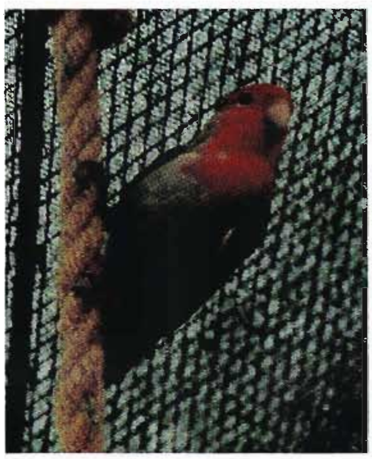


Figure 1.6. Distribution of *Agapornis nigrigenis* in Africa, after Juniper and Parr (1998)

Agapornis roseicollis



The Rosy-faced Lovebird (Figure 1.7) inhabits arid woodland and scrubby hillsides. It is distributed through Angola, Namibia, and South Africa (Figure 1.8). Diet primarily consists of seeds of grasses, *Albizia* and *Acacia*, and the birds are dependent on water (Collar 1997). This species is distributed in an arid environment (Meigs 1953).

Figure 1.7. Rosy-faced Lovebird (*Agapornis roseicollis*)

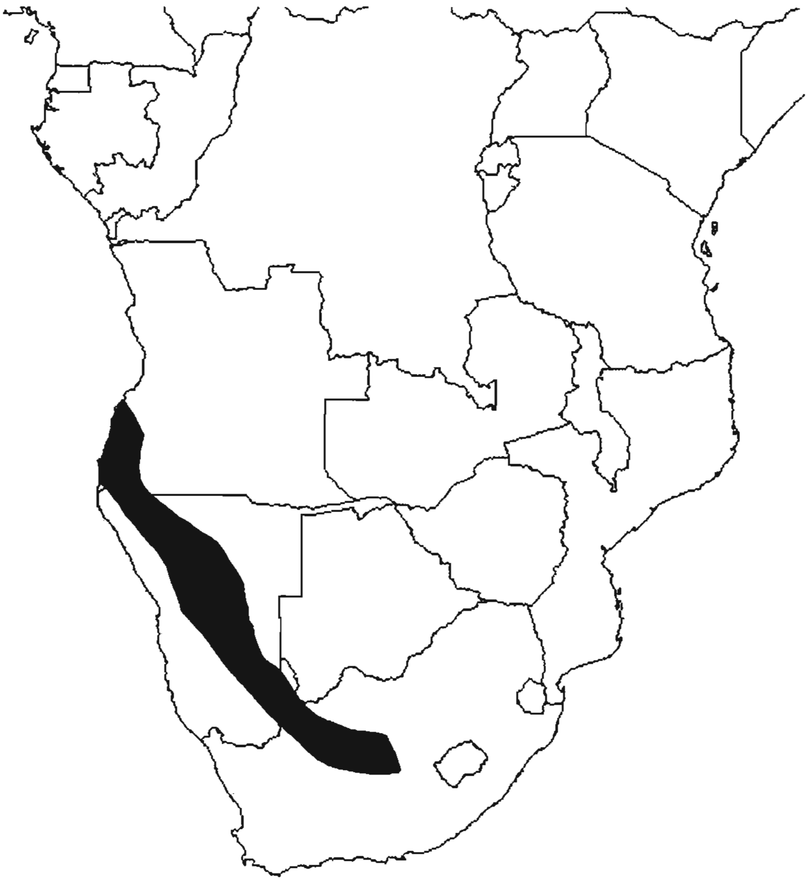


Figure 1.8. Distribution of *Agapornis roseicollis* in Africa, after Juniper and Parr (1998)

Australian Parakeets

Four species of grass parakeet (three *Neophema* and one *Neopsephotus*) were selected as they represented species typifying an aridity gradient, but all from Australia. One species inhabits a mesic area, one species in semi-arid areas, and two species in arid areas (Meigs 1953). These birds represent an independent series to the lovebird subjects, while being similar in size and also granivorous. All species were classified as semi-arid, arid or mesic by Meigs (1953) classification of deserts.

Neopsephotus bourkii

Figure 1.9. Bourke's Parakeet (*Neopsephotus bourkii*)

The Bourke's Parakeet (Figure 1.9) inhabits dry scrubland dominated by *Acacia aneura*. It is distributed through western, central eastern and central southern Australia (Figure 1.10). The diet consists mainly of grass seeds and wild herbs (Collar 1997). This species is distributed in an arid environment (Meigs 1953).

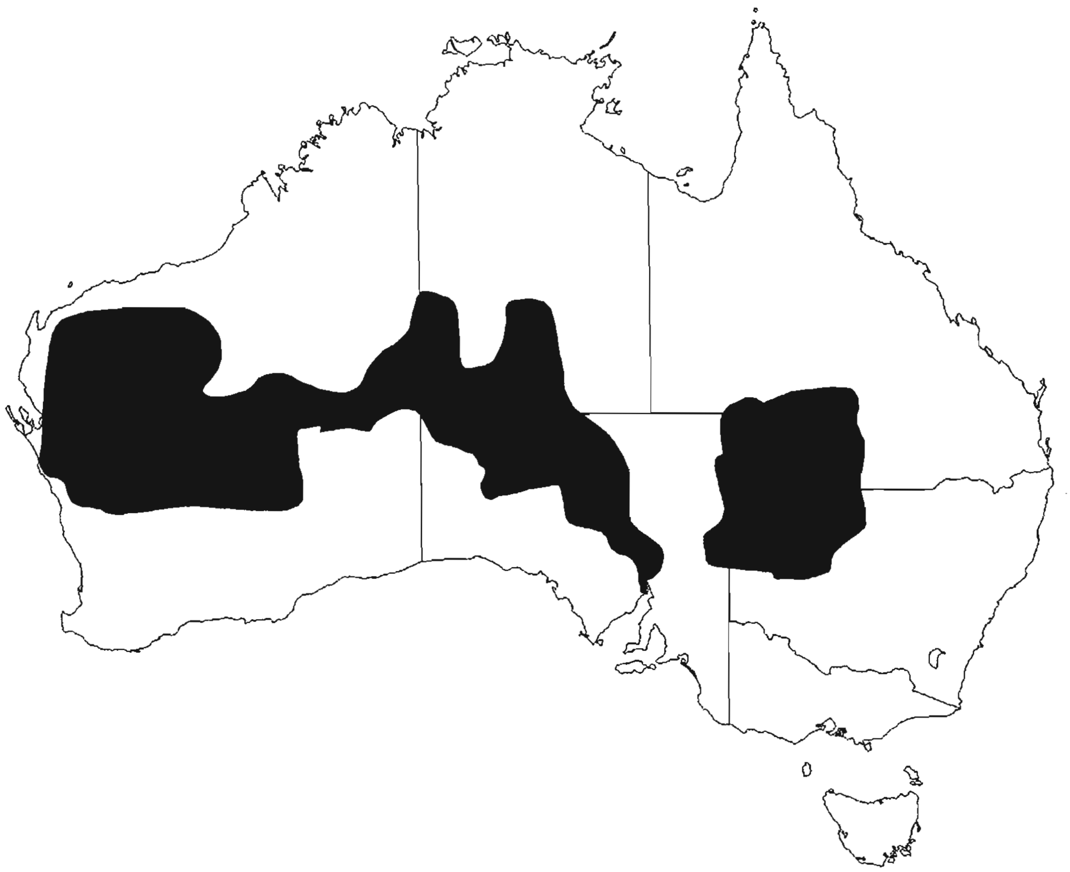
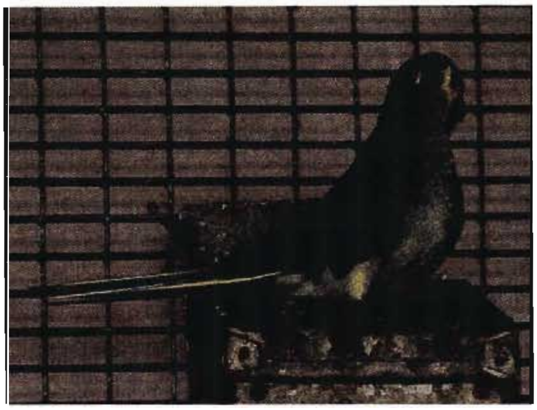


Figure 1.10. **Distribution of *Neopsephotus bourkii* in Australia, after Juniper and Parr (1998)**

Neophema elegans



The Elegant Parakeet (Figure 1.11) inhabits coastal dunes, shrubby grasslands and eucalypt woodlands. It is distributed through south western and south eastern Australia (Figure1.12). The diet consists mainly of grass and tree seeds (Collar 1997). This species is distributed in a semi-arid environment (Meigs 1953).

Figure 1.11. **Elegant Parakeet (*Neophema elegans*)**

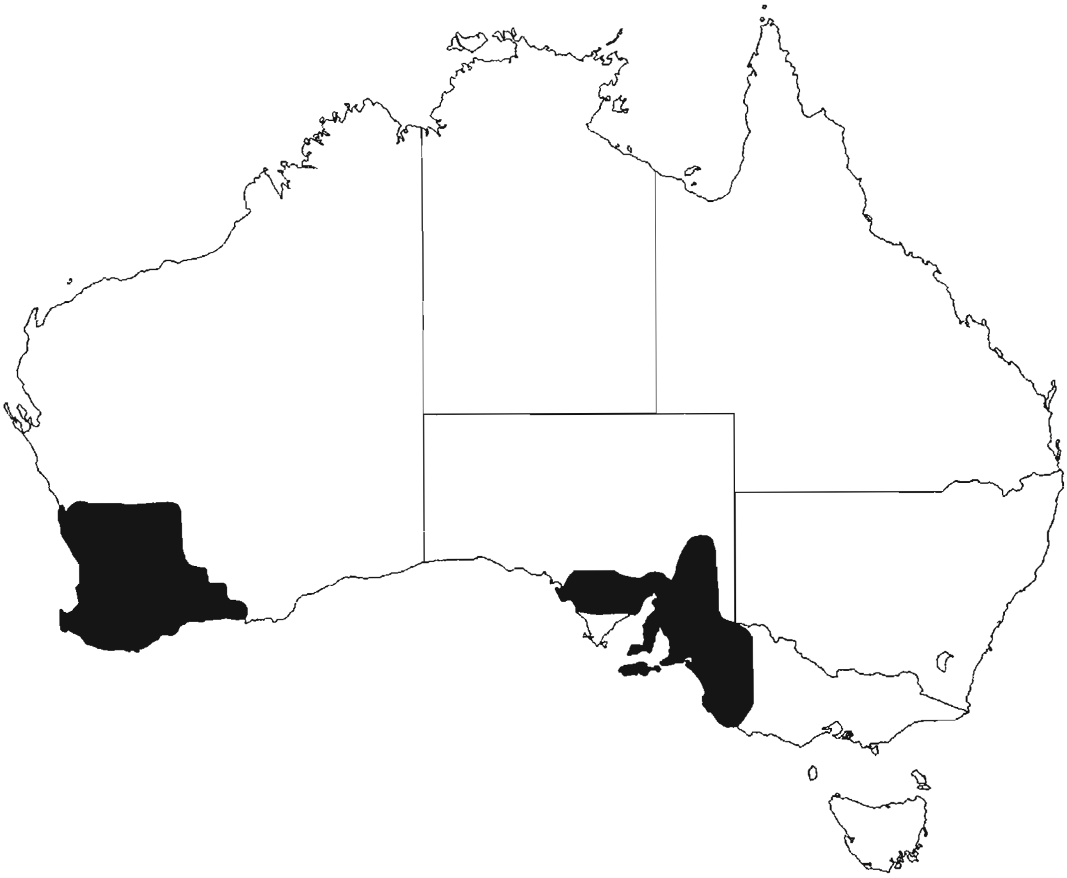
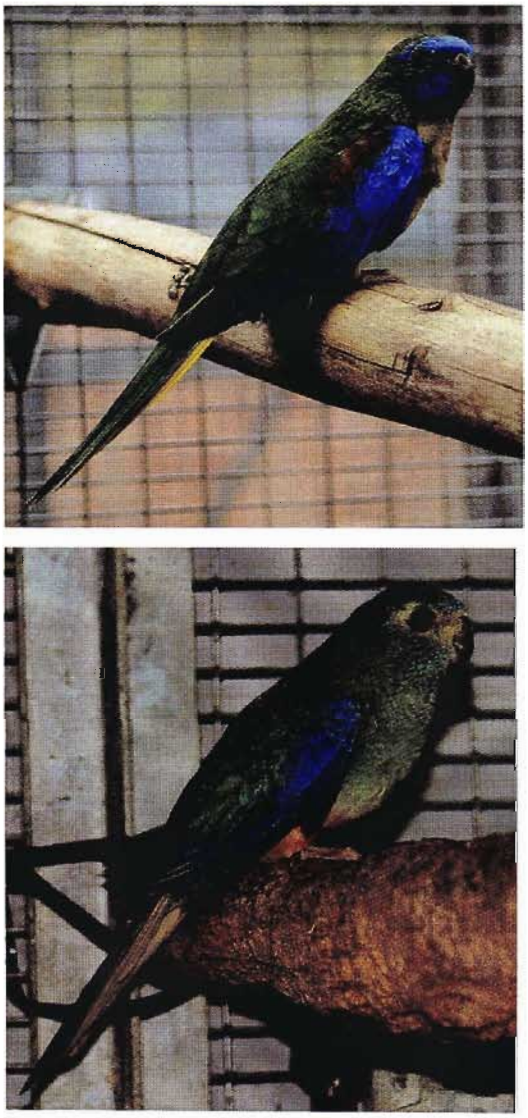


Figure 1.12. **Distribution of *Neophema elegans* in Australia, after Juniper and Parr (1998)**

Neophema pulchella



The Turquoise Parakeet (Figure 1.13) inhabits open forest, woodland and native grassland. It is distributed through south eastern Queensland and northern Victoria, Australia (Figure1.14). The diet consists mainly of seeds, flowers and fruit of grasses and trees (Collar 1997). This species is distributed in a mesic environment (Meigs 1953).

Figure 1.13. Turquoise Parakeet (*Neophema pulchella*), male above and female below

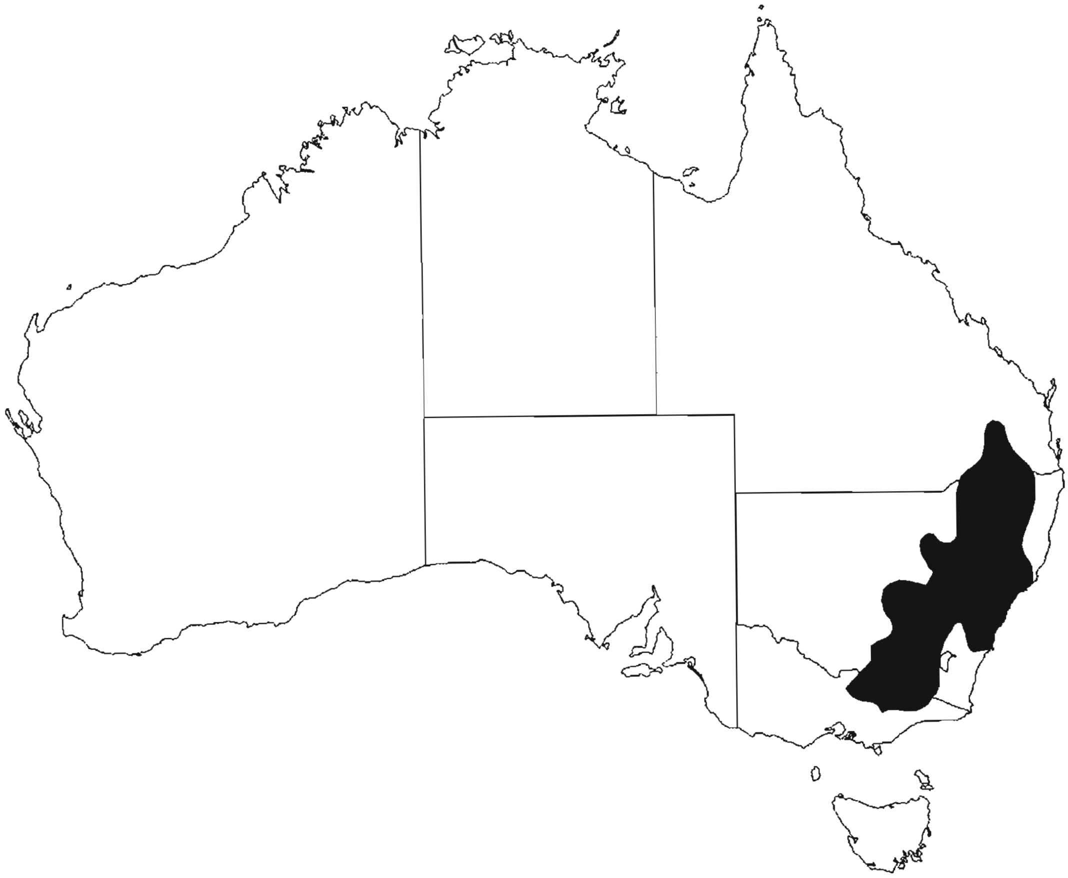
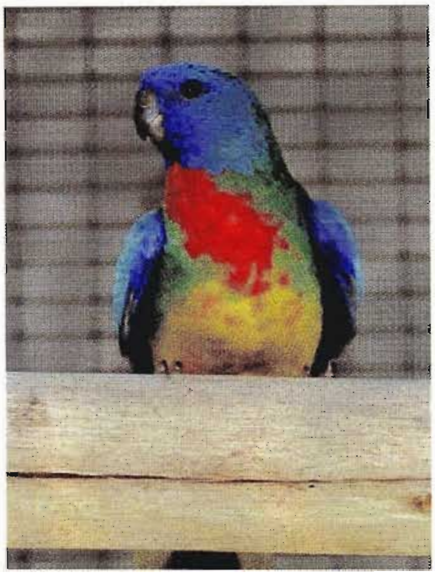


Figure 1.14. **Distribution of *Neophema pulchella* in Australia, after Juniper and Parr (1998)**

Neophema splendida



The Splendid or Scarlet-chested Parakeet (Figure 1.15) inhabits dry *Acacia* scrubland, usually with sparse *Spinifex* cover, and recently burnt areas. It is distributed through the interior of the south western and south eastern Australia (Figure1.16). The diet consists mainly of grass seeds with some tree seeds (Collar 1997). This species is distributed in an arid environment (Meigs 1953).

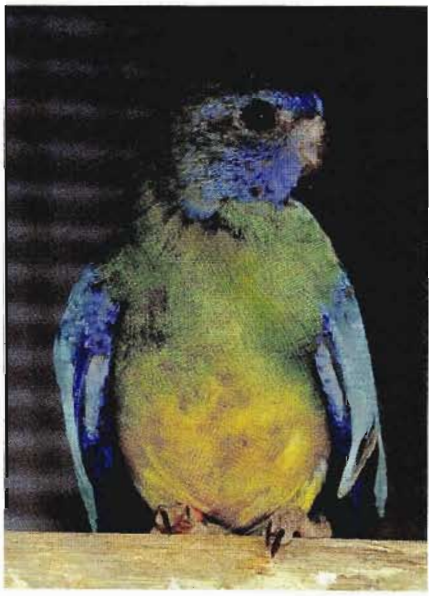


Figure 1.15. Scarlet-chested Parakeet (*Neophema splendida*), male above and female below

Figure 1.16. **Distribution of *Neophema splendida* in Australia, after Juniper and Parr (1998)**

LITERATURE CITED

ANAVA, A., KAM, M., SHKOLNIK, A., & DEGEN, A. A. 2000. Seasonal field metabolic rate and dietary intake in Arabian babblers (*Turdoides squamiceps*) inhabiting extreme deserts. *Functional Ecology* **14**: 607-613.

AUSTIN, G. T. 1976. Behavioral adaptations of the Verdin to the desert. *Auk* **93**: 245-262.

AUSTIN, G. T. 1978. Daily time budget of the postnesting Verdin. *Auk* **95**: 247-251.

BARTHOLOMEW, G. A. & CADE, T. J. 1963. The water economy of land birds. *Auk* **80**: 504-539.

BEISSINGER, S. R., TYGIELSKI, S., & ELDERD, B. 1998. Social constraints on the onset of incubation in a neotropical parrot: a nestbox addition experiment. *Animal Behaviour* **55**: 21-32.

BONADIE, W. A. & BACON, P. R. 2000. Year-round utilisation of a fragmented palm swamp forest by Red-bellied macaws (*Ara manilata*) and Orange-winged parrots (*Amazona amazonica*) in the Nariva Swamp (Trinidad). *Biological Conservation* **95**: 1-5.

BRIGHTSMITH, D., HILBURN, J., DEL CAMPO, A., BOYD, J., FRISIUS, M., FRISIUS, R., JANIK, D., & GUILLEN, F. 2004. The use of hand-raised psittacines for reintroduction: a case study of scarlet macaws (*Ara macao*) in Peru and Costa Rica. *Biological Conservation*

BROECKER, W. S. 1975. Climatic change: are we on the brink of a pronounced global warming? *Science* **189**: 460-463.

BUCHER, T. L. 1981. Oxygen consumption, ventilation and respiratory heat loss in a parrot, *Bolborhynchus lineola*, in relation to ambient temperature. *Journal of Comparative Physiology B* **142**: 479-488.

BUCHER, T. L. 1983. Parrot eggs, embryos, and nestlings: patterns and energetics of growth and development . *Physiological Zoology* **56**: 465-483.

BUCHER, T. L. & MORGAN, K. R. 1989. The effect of ambient temperature on the relationship between ventilation and metabolism in a small parrot (*Agapornis roseicollis*). *Journal of Comparative Physiology* **159**: 561-567.

CHRISTIAN, C. 1993. The challenge of parrot conservation in St Vincent and the Grenadines. *Journal of Biogeography* **20**: 463-469.

CHRISTIAN, C. S., LACHER, T. E., & ZAMORE, M. P. 1996a. Parrot conservation in the lesser antilles with some comparison to the Puerto Rican efforts. *Biological Conservation* **77**: 159-167.

CHRISTIAN, C. S., POTTS, T. D., BURNETT, G. W., & LACHER, T. E. 1996b. Parrot conservation and ecotourism in the Windward Islands. *Journal of Biogeography* **23**: 387-393.

COLLAR, N. J. 1997. Family Psittacidae (Parrots). In: *Handbook of the Birds of the World. Vol. 4. Sandgrouse to Cuckoos,* (eds.) J. del Hoyo, A. Elliot, & J. Sargatal. Lynx Edicions, Barcelona.

COTTON, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences* **100**: 12219-12222.

CRUICKSHANK, A. J., GAUTIER, J-P, & CHAPPUIS, C. 1993. Vocal mimicry in wild african grey parrots *Psittacus erithacus. IBIS* **135**: 293-299.

DAWSON, W. R. 1965. Evaporative water losses of some Australian parrots. *Auk* **82**: 106-108.

DAWSON, W. R. & BENNETT, A. F. 1973. Roles of metabolic level and temperature regulation in the adjustment of Western Plumed Pigeons (*Lophophaps ferruginea*) to desert conditions. *Comparative Biochemistry and Physiology A* **44**: 249-266.

DAWSON, W. R., CAREY, C., ADKISSON, C. S., & OHMART, R. D. 1979. Responses of Brewer's and Chipping Sparrows to water restriction. *Physiological Zoology* **42**: 529-541.

DOWNS, C. T. & SYMES, C. T. 2004. Snag dynamics and forest structure in Afromontane forests in KwaZulu-Natal, South Africa: implications for the conservation of cavity-netsing avifauna. *South African Journal of Botany* **70**: 265-276.

EBERHARD, J. 2002. Cavity adoption and the evolution of coloniality in cavity-nesting birds. *The Condor* **104**: 240-247.

EVANS, P. G. H. 1991. Status and conservation of Imperial and Red-necked Parrots *Amazona imperalis* and *A. arausiaca* on Dominica. *Bird Conservation International* **1**: 11-32.

FARABAUGH, S. M. and DOOLING, R. J. 1996. Acoustic communication in parrots: laboratory and field studies of Budgeriars, *Melopsittacus undulatus*. In: *Ecology and evolution of acoustic communication in birds.*, (eds.) D. E. Kroodsma & E. H. Miller. Cornell University Press, Ithaca.

FISHER, C. D., LINDGREN, E., & DAWSON, W. R. 1972. Drinking patterns and behavior of Australian desert birds in relation to their ecology and abundance. *The Condor* **74**: 111-136.

FORSHAW, J. M. 1977. *Parrots of the World.* T.F.H. Publications, Neptune City, N.J.

FORSHAW, J. M. 2002. *Australian Parrots.* Alexander Editions, Robina.

GIBBS, A. G. 2002. Water balance in desert *Drosophila*: lessons from non-charismatic microfauna. *Comparative Biochemistry and Physiology A* **133**: 781-789.

GLEUCK, F. H. 1994. Illegal exportation of Rüppell's parrots (*Poicephalus rueppellii*) from Namibia. *Avizandum* **Nov**: 4-5.

GNAM, R. & BURCHSTED, A. 1990. Population estimates for the Bahama Parrot on Abaco Island, Bahamas. *Journal of Field Ornithology* **62**: 139-14.

GONZALEZ, J. 2003. Harvesting, local trade, and convservation of parrots in the Northeastern Peruvian Amazon. *Biological Conservation* **114**: 437-446.

HOMBERGER, D. G. 1994. The adaptive radiation of the ecology, bill structure, and feeding mechanism of the Australian Cockatoos as a model for the evolution of seed predation in Psittaciformes. *Journal fur Ornithologie* **135**: 435-

INOUYE, D. W., BARR, B., ARMITAGE, K. B., & INOUYE, B. D. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences* **97**: 1630-1633.

IPCC 2001. *Climate change 2001: Third assessment report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge.

JOSEPH, L. 1988. A review of the conservation status of Australian parrots in 1987. *Biological Conservation* **46**: 261-280.

JUNIPER, T. & PARR, M. 1998. *Parrots: a guide to the parrots of the world.* Pica Press, Sussex.

KAM, M., ANAVA, A., SHKOLNIK, A., & DEGEN, A. A. 2003. Energy expenditure and its components in free-living arabian babblers (*Turdoides squamiceps*). *Israel Journal of Zoology* **49**: 195-202.

KONARZEWSKI, M. & DIAMOND, J. 1995. Evolution of basal metabolic rate and organ masses in laboratory mice. *Evolution* **49**: 1239-1248.

LAMBERT, F. R. 1993. Trade, status, and management of three parrots in the North Moluccas,Indonesia: White Cockatoo *Cacatua alba*, Chattering Lory *Lorius garrulus*and Violet-eared Lory *Eos squamata. Bird Conservation International* **3**: 145-168.

LINDGREN, E. 1973. *Studies in the ecology and physiology of three species of grass-parrots (Neophema. Aves: Psittacidae)*. PhD thesis. University of Western Australia

LINDSEY, G. D. 1992. Nest guarding from observation blinds: strategy for improving Puerto Rican parrot nest success. *Journal of Field Ornithology* **63**: 466-472.

LOW, R. 1984. *Endangered parrots*. Blandford Press, Dorset.

MACLEAN, G. L. 1996. *Ecophysiology of Desert Birds*. Springer-Verlag, Berlin Heidelberg.

MACMILLEN, R. E. 1990. Water economy of granivorous birds: a predictive model. *The Condor* **93**: 379-392.

MARSDEN, S. J. & JONES, M. J. 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biological Conservation* **82**: 279-287.

MCGINNIES, W. G.1979.Description and structure of arid ecosystems: general description of desert areas. *Arid-land Ecosystems: Structure, Functioning and Management*, (eds) Goodall, D. W., F. A. Perry, and K. W. Howes. Cambridge University Press, Cambridge.

MCKECHNIE, A. E. & WOLF, B. O. 2004. The allometry of avian basal metabolic rate: good predictions need good data. *Physiological and Biochemical Zoology* **77**: 502-521.

MEIGS, P. 1953. *Reviews of Research on Arid Zone Hydrology*. UNESCO, Paris.

MILLAM, J. R., ROUDYBUSH, T. E., & GRAU, C. R. 1988. Influence of environmental manipulation and nest-box availability on reproductive success of captive cockatiels (*Nymphicus hollandicus*). *Zoo Biology* **7**: 25-34.

MOLLER, A. P. 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* **63**: 309-311.

NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* **57**: 111-128.

NAGY, K. A., GIRARD, I. A., & BROWN, T. K. 1999. Energetics of free-ranging mammal, reptiles, and birds. *Annual Review of Nutrition* **19**: 247-277.

NAGY, K. A. & PETERSON, C. C. 1988. *Scaling water flux rate in animals.* University of California Publications in Zoology, I.

NOY-MEIR, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**: 25-41.

PARMESAN, C. & YOHE, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37-42.

PEÑUELAS, J. & FILELLA, I. 2001. Responses to a warming world. *Science* **294**: 793-794.

PERRIN, M. 2002. Cape Parrots and Yellowwood trees: wanted dead or alive! *Avizandum* **14**: 6-8.

PIERSMA, T., BRUINZEEL, L., DRENT, R., KERSTEN, M., VAN DER MEER, J., & WIERSMA, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* **69**: 191-217.

PROZESKY, O. P. M. 1978. Parrots bright and beautiful. *Fauna & Flora* **33**: 2-5.

RICKLEFS, R. E. & HAINSWORTH, F. R. 1968. Temperature dependent behavior of the cactus wren. *Ecology* **49**: 227-233.

ROBINSON, L. 1996. Turquoise Parrots *Neophema pulchella* -30 years on. *Eclectus* 14-16.

ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C., & POUNDS, J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57-60.

SANZ, J. J., POTTI, J., MORENO, J., MERINO, S., & FRIAS, O. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology* **9**: 461-472.

SANZ, V. & GRAJAL, A. 1998. Successful reintroduction of captive-raised Yellow-shouldered Amazon parrots on Margarita Island, Venezuela. *Conservation Biology* **12**: 430-441.

SCHLEUCHER, E., PRINZINGER, R., & WITHERS, P. C. 1991. Life in extreme environments: Investigations on the ecophysiology of a desert bird, the Australian Diamond Dove (*Geopelia cuneata* Latham). *Oecologia* **88**: 72-76.

SCHMIDT-NIELSEN, K. 1984. *Animal Physiology: Adaptation and Environment.* Cambridge University Press, Cambridge.

SHMIDA, A. 1985. Biogeography of the desert flora. In: *Hot Deserts and Arid Shrublands,* (eds.) M. Evenari, I. Noy-Meir, & D. W. Goodall. Elsevier, Amsterdam.

SILVIUS, K. M. 1997. What it takes to save a parrot. *Wildlife conservation* **100**: 53-66.

SNYDER, N., MCGOWAN, P., GILARDI, J., and GRAJAL, A. 2000. *Parrots. Status survey and conservation action plan 2000-2004.* IUCN, Gland, Switzerland.

STOLTZ, L. 1994. *Managing and regulating the parrot industry in South Africa.* Museum of Natural History, Vienna.

THORNTHWAITE, C. W. 1948. An approach toward a rational classification of climate. *Geographical Reviews* **38**: 55-94.

TIELEMAN, B. I. & WILLIAMS, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**: 461-479.

TIELEMAN, B. I., WILLIAMS, J. B., & VISSER, G. H. 2003. Variation in allocation of time, water and energy in hoopoe larks from the Arabian Desert. *Functional Ecology* **17**: 869-876.

WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia* **42**: 81-89.

WEAVER, CM 1987. A comparison of temperatures recorded in nest chambers excavated in termite mounds by the Golden-shouldered Parrot. *Emu* **87**: 57-59.

WEBSTER, M. D. 1991. Behavioral and Physiological adaptations of birds to hot desert climates, In: *Proceedings of the 20th International Ornithological Congress*: 1765-1776. Christchurch, New Zealand.

WIKELSKI, M., SPINNEY, L., SCHELSKY, W., SCHEUERLEIN, A., & GWINNER, E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B* **270**: 2383-2388.

WILLIAMS, J. B. 1999. Heat production and evaporative water loss of dune larks from the Namib desert. *Condor* **101**: 432-438.

WILLIAMS, J. B., BRADSHAW, D., & SCHMIDT, L. 1995. Field metabolism and water requirements of Spinifex Pigeons (*Geophaps plumifera*) in Western Australia. *Australian Journal of Zoology* **43**: 1-15.

WILLIAMS, J. B., TIELEMAN, B. I., & SHOBRAK, M. 1999. Lizard burrows provide thermal refugia for larks in the Arabian desert. *Condor* **101**: 714-717.

WILLIAMS, J. B., WITHERS, P. C., BRADSHAW, S. D., & NAGY, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Australian Journal of Zoology* **39**: 131-142.

WING, S. L., HARRINGTON, G. J., SMITH, F. A., BLOCH, J. I., BOYER, D. M., & FREEMAN, K. H. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* **310**: 993-996.

WITHERS, P. C. & WILLIAMS, J. B. 1990. Metabolic and respiratory physiology of an arid-adapted Australasian bird, the Spinifex pigeon. *Condor* **92**: 961-969.

WOLF, B. O. 2000. Global warming and avian occupancy of hot deserts: a physiological and behavioral perspective. *Revista Chilena de Historia Natural* **75**: 387-392.

WOLF, B. O., MARTINEZ DEL RIO, C., & BABSON, J. 2002. Stable isotopes reveal that saguaro fruit provides different resources to two desert dove species. *Ecology* **83**: 1286-1293.

WOLF, B. O. & WALSBERG, G. E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* **77**: 2228-2236.

WOLF, B. O., WOODEN, K. M., & WALSBERG, G. E. 1996. The use of thermal refugia by two small desert birds. *Condor* **98**: 424-428.

WRIGHT, T. F., TOFT, C. A., ENKERLIN-HOEFLICH, E., GONZALEZ-ELIZONDO, J., ALBORNOZ, M., RODRIGUEZ-FERRARO, A., ROJAS-SUAREZ, F., SANZ, V., TRUJILLO, A., BEISSINGER, S. R., BEROVIDES, V. A., GALVEZ, X. A., BRICE, A. T., JOYNER, K., EBERHARD, J., GILARDI, J., KOENIG, S. E., STOLESON, S., MARTUSCELLI, P., MEYERS, J. M., RENTON, K., RODRIGUEZ, A. M., SOSA-ASANZA, A. C., VILELLA, F. J., & WILEY, J. W. 2001. Nest poaching in neotropical parrots. *Conservation Biology* **15**: 710-720.

CHAPTER TWO

THERMAL BIOLOGY OF AFRICAN & AUSTRALIAN PARROTS

INTRODUCTION

Deserts are characterised by high ambient temperatures (T_a) and low rainfall, and thus low primary productivity (Fisher et al. 1972; Williams et al. 1991; Tieleman et al. 2003). This combination of factors makes deserts one of the most extreme environments on the planet, and means that animals and plants living in these ecosystems are faced with unique challenges in order to survive (Fisher et al. 1972; Louw & Seely 1982). The most obvious problems associated with living in these harsh habitats are the high T_as, the lack of free standing water, and the scarcity of food resources (Williams et al. 1991; Tieleman & Williams 2000; Gibbs 2002). For species to survive and breed in deserts, adaptations may have evolved to overcome these problems (Dawson & Bennett 1973). The reduction of basal metabolic rates (BMR) in desert dwelling birds, in comparison with more mesic dwelling birds, has been shown in several species (Trost 1972; Dawson & Bennett 1973; Thomas & Maclean 1981; Goldstein & Nagy 1985; Withers & Williams 1990; Tieleman et al. 2003). Explanations for the evolution of decreased BMRs include the idea that reduced metabolic rates correlate with a reduced food requirement, and reduced respiratory frequency (Dawson & Bennett 1973). Reduced food intake is obviously of survival value in a habitat with low productivity, and reduced respiratory frequency implies reduced pulmonary water loss, and hence water conservation (Dawson & Bennett 1973). However, the idea that physiological adaptations have evolved in birds living in deserts has sometimes been queried (Bartholomew & Cade 1963; Maclean 1996). In response to this resistance to the idea that low BMRs have evolved in some birds, Tieleman and Williams (2000) performed the most extensive analysis of desert versus non-desert bird BMRs to date. They found a significant reduction in the BMR of desert birds when compared with non-desert species. However, the debate continues as to whether this reduction is indeed a physiological adaptation, or evidence for BMR being subject to phenotypic plasticity. There is however a disadvantage to lower BMRs in hot deserts, as they are generally accompanied by lower body temperatures (T_b). A lower T_b means a smaller ($T_b - T_a$) gradient over which the bird can lose heat to the environment by convective and radiative processes.

Parrots typically inhabit tropical and sub-tropical forests and are identified by their bright plumage, fleshy cere, zygodactylous feet, and unique bill structure and shape (Forshaw 1977; Collar 1997; Juniper & Parr 1998). However, on the continents of Africa and Australia several species of parrot have left the forests, and some have even invaded the deserts of these continents (Juniper & Parr 1998). Most of the species inhabiting open woodland and deserts are granivorous (Homberger 1994). However, the majority of these non-forest parrot species are still dependent on trees for breeding, as they are secondary cavity nesters (Eberhard 2002; Downs & Symes 2004).

I tested the idea that desert dwelling parrots have lower BMRs than non-desert dwelling parrots. The study was based in the laboratory to remove the effects of the environment, and so allow cross-species comparisons without the confounding effect of habitat differences (Wikelski et al. 2003).

METHODS

Birds and Experimental Conditions

Four species of African lovebirds (*Agapornis* species), and four species of Australian grass parakeets (one *Neopsephotus* and three *Neophema* species) were chosen for experimentation because they inhabit a range of habitats representing an aridity gradient, as defined by Meigs's (1953) classification of desert environments. Meigs (1953) classified desert environments into mesic, semi-arid, arid and hyper-arid using Thornwaite's (1948) index of moisture availability (I_m). The I_m is calculated using precipitation, the maximum ambient air temperature (T_a) of the hottest month of the year, and the minimum T_a of the coldest month of the year (Thornthwaite 1948). The Rosy-faced Lovebird (*A. roseicollis*) was categorised as an arid zone species, Fischer's Lovebird (*A. fischeri*) and the Yellow-collared Lovebird (*A. personatus*) were categorised as semi-arid zone species, and the Black-cheeked Lovebird (*A. nigrigenis*) as a mesic zone species. The Bourke's Parakeet (*Neopsephotus bourkii*) and the Scarlet-chested Parakeet (*Neophema splendida*) were categorised as arid zone species, the Elegant Parakeet (*N. elegans*) was categorised as a semi-arid zone species, and the Turquoise Parakeet (*N. pulchella*) as a mesic zone species. Four or five birds of each species (sourced from breeders in KwaZulu-Natal) were housed in temperature controlled rooms in the Animal House at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg. Birds were fed *ad libitum* on a diet of sunflower and mixed millet seeds, supplemented with a mix of greens consisting of spinach, apple, beetroot, carrot, corn and broccoli. Rooms were set at T_a = 25 °C with a photoperiod of 12L:12D for the duration of the study. Experiments were carried out during September to December 2005.

Metabolic Measurements

Oxygen consumption (VO_2) was measured as an indirect quantification of metabolic rate. Measurements were made in respirometers constructed from clear Perspex® under a 12L:12D photoperiod (matched to the temperature controlled rooms). Respirometer volume was 3.96 l (22cm high, 12cm wide and 15cm long) and included a perch for the bird. All respirometers were placed within a temperature controlled sound-proof cabinet. T_a within the cabinet was measured using thermistor probes calibrated with a standard mercury thermometer (0.05 °C) in a water bath at temperatures from 5 - 45 °C.

VO_2 was measured using an open flow-through system. Atmospheric air, acting as the control gas, was pumped from outside the building, partially dried using silica gel, into the temperature controlled cabinet. Air was drawn through the respirometers at flow rates that ensured that the depletion of oxygen between incurrent and excurrent air was maintained at less than one percent (ca. 0.8 l min^{-1}). The air flow entered the bottom of each respirometer, and exited at the top, to maintain a constant flow of air past the birds. By using solenoid valves and a separate pump for each respirometer, simultaneous measurement of five experimental and one control chamber was achieved. The flow rate of each of the chambers was measured using a Brooks thermal mass flow meter (Model 5860E) factory calibrated to STP.

The excurrent air from each respirometer passed through a water condenser (a copper tube in which the air was cooled to approximately 3°C, or below dew point) to remove water vapour, and a CO_2 scrubber (soda lime) to remove CO_2 gas. After passing through the pumps, solenoids, filters and the mass flow meter, the excurrent air was sub sampled with an oxygen analyser (Model S-3A/1, Ametek) to determine the fractional concentration of oxygen in the dry air. The fractional concentration of O_2 in the control chamber was measured at the beginning of every five minute cycle, and the O_2 measurements from the experimental chambers were then subtracted from this control value. The problem of long-term drift in O_2 analyser outputs was thus limited to that which could occur in six minutes, and therefore allowed long-term measurements of VO_2.

Analog signals from the thermistor probes, mass flow meter and oxygen analyser were digitised using an A/D converter and recorded on a multi-channel WINDOWS-based recording programme (Robert Van Zyl pers. comm.). Measurements of the various parameters for each chamber (T_a, flow rate and fractional O_2 concentration) were recorded at the end of the 45 second sampling interval, so as to allow sufficient time for the flushing of air from the previous channel from the ducting between the relay valves and the sub sample tubing. Oxygen consumption was calculated using the equation:

$$VO_2 = V_E\,(F_{I\,O2} - F_{E\,O2}) \,/\, (1 - F_{I\,O2}) \text{..........................equation (1)}$$

where VO_2 = metabolic rate (ml O_2 h^{-1}), V_E = flow rate (ml min^{-1}), $F_{I\,O2}$ = incurrent fractional O_2 concentration and $F_{E\,O2}$ = excurrent fractional O_2 concentration (Withers 1977). Birds were weighed before and after each experiment and mass specific VO_2 was thus calculated by altering equation (1) to include body mass:

$$VO_2 = \frac{V_E\,(F_{I\,O2} - F_{E\,O2}) \,/\, (1 - F_{I\,O2})}{M_b} \text{..................................equation (2)}$$

Where VO_2 = mass specific metabolic rate (ml O_2 g^{-1} h^{-1}), V_E, $F_{I\,O2}$ and $F_{E\,O2}$ remain the same, and M_b = body mass (g) (Withers 1977).

Experimental Protocol

Birds were placed individually in the respirometers at ca. 16h30, to allow sufficient time to equilibrate before the onset of the rest-phase. They were removed from the respirometers an hour after lights-on the following morning (± 07h00), ensuring that VO_2 attained normothermic active-phase levels. Birds were returned to their cages after experimentation and immediately fed and supplied with fresh water. Measurements of VO_2 were captured for 4 - 5 birds of each species at T_a = 5, 10, 15, 20, 25, 28, 32 and 35 °C. The birds were maintained in the respirometers for the entire rest-phase at each T_a, except T_a = 35°C where the birds exhibited excessive evaporative water loss and heavy panting and so were taken out of the respirometers at ca. 20h45 to reduce the chances of mortality. Birds of each species were measured at T_a = 25 °C on their first night of testing to habituate them to the respirometers. Birds and temperatures were randomised for all species. The data from these initial measurements were not used for any analyses, and the birds were measured again under the same conditions at T_a = 25 °C to collect data.

Phylogenetic Effect

It has been argued that the comparison of data across species by conventional means violates the statistical assumption of independence by virtue of the relatedness of these species in a phylogenetic framework (Felsenstein 1985; Cheverud et al. 1985; Harvey & Pagel 1991). Data points for differences in BMR and body mass were analysed using conventional analyses, but also using phylogenetically independent contrasts (PIC), that resolve this problem, rendering each data point independent (Felsenstein 1985). A phylogeny for the parrots under investigation was constructed from the literature, using both molecular and morphological characteristics (Moreau 1948; Leeton et al. 1994; Williams 1996; Collar 1997; Eberhard 1998), as a molecular phylogeny for all the species studied is not available. PDTREE was used to create the phylogeny and calculate the PICs (Garland et al. 1992). In order to adequately standardise contrasts (Garland et al. 1992) the phylogeny branch lengths were transformed using the arbitrary branch length method of Pagel (1992).

Data Analysis

VO_2 was recorded eight times per hour for each bird. Mean hourly VO_2 values were calculated using each value for each individual ($n = 4$ or 5). Minimum and maximum mean hourly VO_2 values were determined using those mean values. STATISTICA (Statsoft, Tulsa, Oklahoma) software was used for statistical analyses. Values recorded for each individual were used in tests using repeated-measures ANOVA. Means are presented ± 1 SD. Estimates of the lower critical limit of thermoneutrality (T_{lc}) were calculated by piece-wise linear regression conducted in R (R Development Core Team 2006). Comparative analyses were carried out in PDSINGLE, PDANOVA and PDSIMUL (Garland et al. 1992; Garland et al. 1993). BMR and M_b data were log transformed prior to phylogenetic analyses. The BMR for each species was taken as the lowest minimum VO_2 for any T_a.

RESULTS

African Lovebirds

There was no significant difference in daily body mass of individuals between trials at the various T_as for any of the lovebird species (RMANOVA, $F_{(7,32)} = 0.08$, $P > 0.05$; RMANOVA, $F_{(7,32)} = 0.09$, $P > 0.05$; RMANOVA, $F_{(7,32)} = 0.43$, $P > 0.05$; RMANOVA, $F_{(7,32)} = 0.96$, $P > 0.05$; for *A. fischeri*, *A. nigrigenis*, *A. personatus* and *A. roseicollis* respectively). Minimum VO_2 differed significantly with changes in T_a for all species (RMANOVA, $F_{(6,336)} = 603.9$, $P < 0.01$; RMANOVA, $F_{(6,360)} = 836.97$, $P < 0.01$; RMANOVA, $F_{(6,336)} = 695.4$, $P < 0.01$; RMANOVA, $F_{(6,336)} = 997.7$, $P < 0.01$; for *A. fischeri*, *A. nigrigenis*, *A. personatus* and *A. roseicollis* respectively).

Below $T_a = 25$°C the minimum VO_2 of all species increased rapidly, whereas above this T_a minimum VO_2 remained relatively constant up to 35°C (Figure 2.1). Minimum and maximum VO_2 were taken as the lowest and highest hourly average for all individuals of a species (Table 2.1). VO_2 did not fluctuate excessively during the rest phase for any species at any T_a, as is evident in the data for *A. fischeri* (Figure 2.2). The BMR of *A. roseicollis* (arid zone species) was the lowest, with *A. personatus* and *A. fischeri* (semi-arid zone species) having slightly higher BMRs, and *A. nigrigenis* (mesic zone species) having the highest BMR of the *Agapornis* species (Table 2.1).

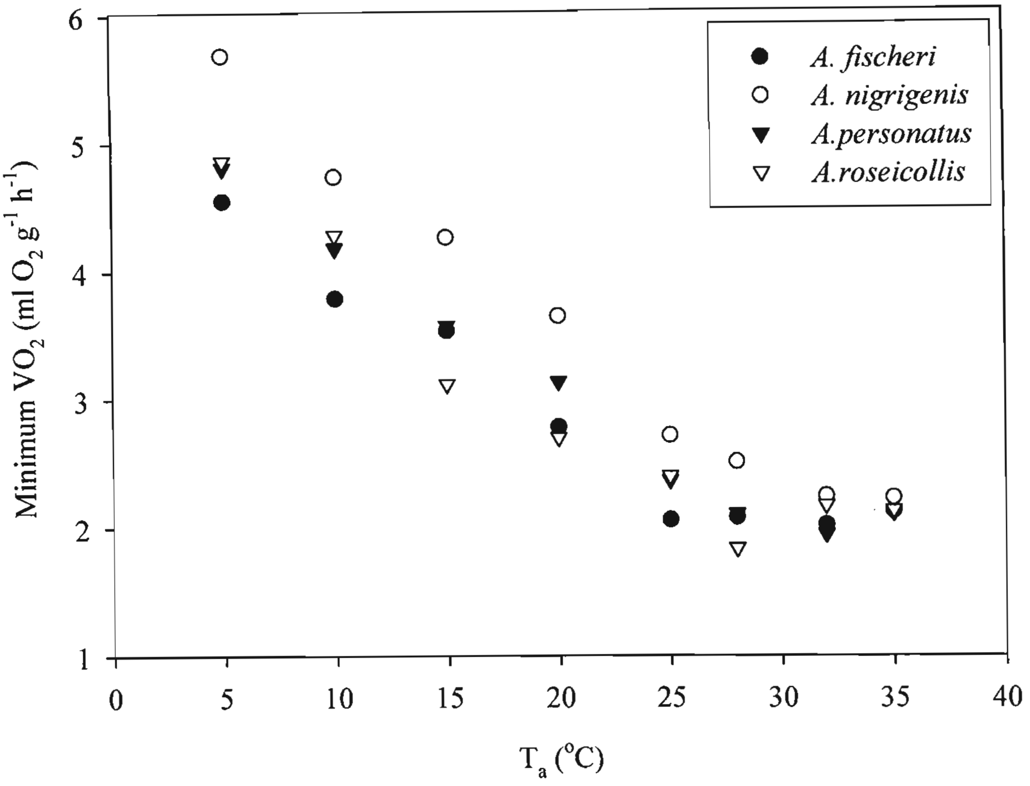


Figure 2.1 Minimum VO$_2$ (means) of *Agapornis* spp. with respect to ambient temperature. Measured during rest phase.

Australian Parakeets

There was no significant difference in daily body mass of individuals between trials at the various T$_a$s for any of the Parakeet species (RMANOVA, $F_{(7,32)} = 0.05$, $P > 0.05$; RMANOVA, $F_{(7,32)} = 0.44$, $P > 0.05$; RMANOVA, $F_{(7,24)} = 0.30$, $P > 0.05$; RMANOVA, $F_{(7,24)} = 0.27$, $P > 0.05$; for *N. bourkii*, *N. splendida*, *N. pulchella* and *N. elegans* respectively). Minimum VO$_2$ differed significantly with changes in T$_a$ for all species (RMANOVA, $F_{(6,336)} = 714.9$, $P < 0.01$; RMANOVA, $F_{(6,360)} = 1067.4$, $P < 0.01$; RMANOVA, $F_{(6,270)} = 237.9$, $P < 0.01$; RMANOVA, $F_{(6,270)} = 508.7$, $P < 0.01$; for *N. bourkii*, *N. splendida*, *N. pulchella* and *N. elegans* respectively).

Table 2.1 Mean oxygen consumption (VO_2) (± SD) of *Agapornis* spp. in relation to ambient temperature. Percent reduction refers to min and max values presented.

Species	Ambient temperature (°C)	Min. VO_2 (β) (ml O_2 g^{-1} h^{-1})	Max. VO_2 (α) (ml O_2 g^{-1} h^{-1})	Change in VO_2 (ml O_2 g^{-1} h^{-1}) (Max-Min)	% reduction in MR
A. nigrigenis	5	5.68 ± 0.61	8.40 ± 0.94	2.72	32.4
	10	4.74 ± 0.30	7.87 ± 0.93	3.13	39.8
	15	4.26 ± 0.50	6.71 ± 0.44	2.45	36.5
	20	3.65 ± 0.19	6.63 ± 0.92	2.99	45.0
	25	2.71 ± 0.28	5.53 ± 0.41	2.82	51.0
	28	2.51 ± 0.14	4.22 ± 0.16	1.72	40.7
	32	2.24 ± 0.14	3.35 ± 0.44	1.11	33.1
	35	2.22 ± 0.16	3.46 ± 0.18	1.24	35.8
A. fischeri	5	4.55 ± 0.33	6.53 ± 0.44	1.98	30.3
	10	3.79 ± 0.21	6.32 ± 1.32	2.53	40.0
	15	3.54 ± 0.25	7.12 ± 0.37	3.58	50.3
	20	2.78 ± 0.21	6.19 ± 1.37	3.41	55.1
	25	2.05 ± 0.11	4.29 ± 0.43	2.23	52.1
	28	2.07 ± 0.20	4.77 ± 0.55	2.69	56.5
	32	2.01 ± 0.18	3.99 ± 0.78	1.97	49.5
	35	2.12 ± 0.17	2.67 ± 0.13	0.55	20.5
A. personatus	5	4.81 ± 0.53	7.75 ± 0.54	2.94	37.9
	10	4.18 ± 0.58	6.86 ± 0.74	2.68	39.1
	15	3.57 ± 0.25	6.81 ± 0.86	3.24	47.6
	20	3.13 ± 0.38	5.90 ± 0.40	2.76	46.9
	25	2.36 ± 0.31	4.92 ± 0.63	2.55	51.9
	28	2.10 ± 0.33	5.10 ± 0.68	3.00	58.8
	32	1.94 ± 0.19	4.14 ± 0.82	2.20	53.1
	35	2.11 ± 0.15	3.81 ± 0.58	1.70	44.7
A. roseicollis	5	4.86 ± 0.44	7.16 ± 0.69	2.30	32.1
	10	4.28 ± 0.39	6.76 ± 0.58	2.48	36.7
	15	3.11 ± 0.26	5.51 ± 0.37	2.40	43.5
	20	2.69 ± 0.21	5.54 ± 0.60	2.85	51.4
	25	2.39 ± 0.20	4.37 ± 0.43	1.97	45.2
	28	1.83 ± 0.19	3.62 ± 0.29	1.78	49.3
	32	2.17 ± 0.10	3.52 ± 0.64	1.36	38.5
	35	2.13 ± 0.16	3.48 ± 0.22	1.35	38.9

α – active phase. β - rest phase.

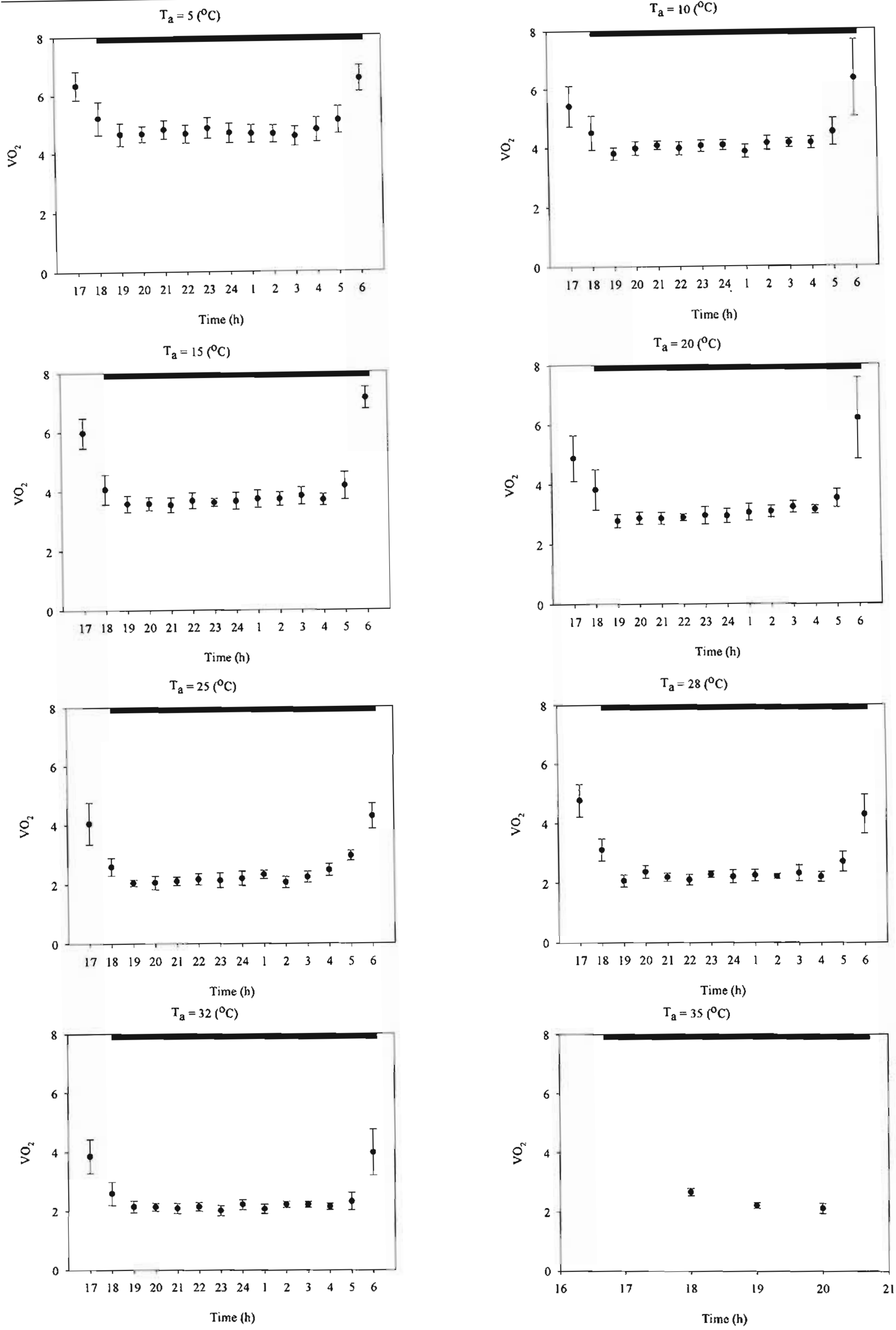


Figure 2.2 Change in oxygen consumption (VO_2, measured in ml O_2 g^{-1} h^{-1}) of *A. fischeri* with time for the various ambient temperatures (T_a) (mean ± SD, $n = 5$)

Below T_a = 25°C the minimum VO_2 of all species increased rapidly, while above this T_a minimum VO_2 remained relatively constant up to 35°C (Figure 2.3). Minimum and maximum VO_2 were taken as the lowest and highest hourly average for all individuals of a species (Table 2.2). VO_2 did not fluctuate excessively during the rest phase for any species at any T_a, as is evident in the data for *N. bourkii* (Figure 2.4). The BMR of *N. bourkii* (arid zone species) was the lowest, with *N. splendida* (arid zone species) having a slightly higher BMR, *N. elegans* (mesic zone species) has the next highest BMR and *N. pulchella* (semi-arid zone species) has the highest BMR of the parakeets (Table 2.2).

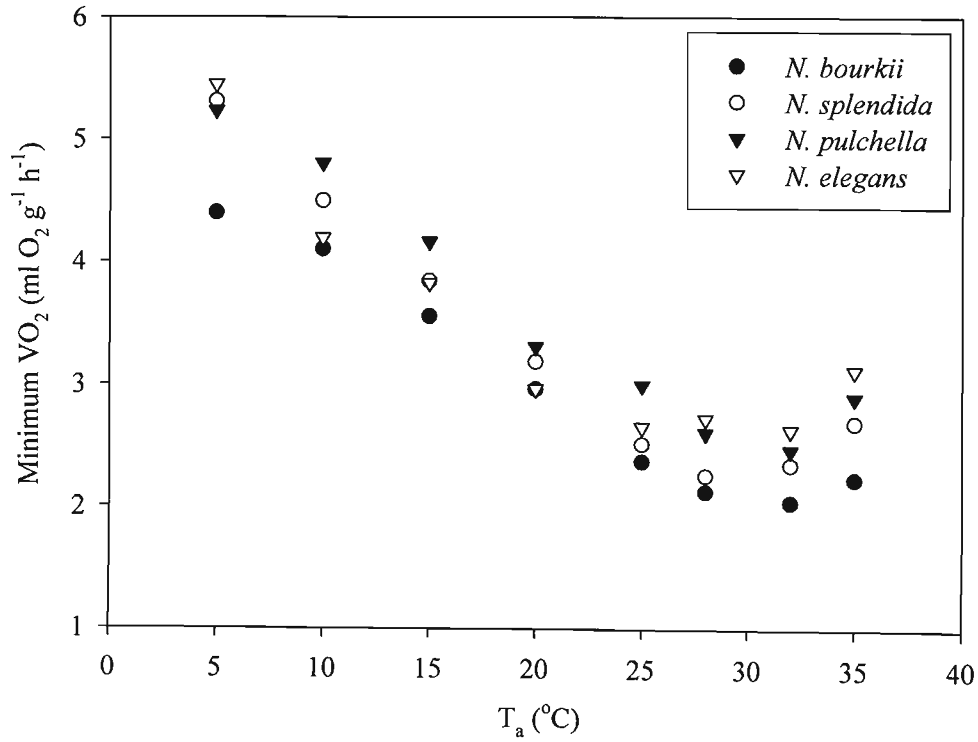


Figure 2.3 Minimum VO_2 (means) of *Neophema* and *Neopsephotus* spp. with respect to ambient temperature. Measured during rest phase.

Table 2.2 Mean oxygen consumption (VO_2) (± SD) of *Neophema* and *Neopsephotus* spp. in relation to ambient temperature. Percent reduction refers to min and max values presented.

Species	Ambient temperature (°C)	Min. VO_2 (β) (ml O_2 g^{-1} h^{-1})	Max. VO_2 (α) (ml O_2 g^{-1} h^{-1})	Change in VO_2 (ml O_2 g^{-1} h^{-1}) (Max-Min)	% reduction in MR
N. pulchella	5	5.23 ± 0.35	9.01 ± 1.25	3.78	42.0
	10	4.80 ± 0.72	8.72 ± 0.86	3.92	44.9
	15	4.16 ± 0.62	8.52 ± 0.90	4.36	51.1
	20	3.31 ± 0.12	7.33 ± 0.59	4.02	54.8
	25	3.00 ± 0.37	6.92 ± 1.12	3.92	56.7
	28	2.61 ± 0.59	5.58 ± 0.68	2.97	53.2
	32	2.47 ± 0.12	5.52 ± 0.80	3.04	55.2
	35	2.90 ± 0.29	4.01 ± 0.67	1.11	27.8
N. elegans	5	5.45 ± 0.73	8.48 ± 1.48	3.03	35.7
	10	4.19 ± 0.80	7.59 ± 1.55	3.40	44.8
	15	3.83 ± 0.36	7.12 ± 1.14	3.29	46.3
	20	2.97 ± 0.32	5.00 ± 0.57	2.04	40.7
	25	2.66 ± 0.22	4.67 ± 0.58	2.01	43.0
	28	2.73 ± 0.21	4.40 ± 0.40	1.67	38.0
	32	2.63 ± 0.34	4.46 ± 0.60	1.82	40.9
	35	3.12 ± 0.27	3.33 ± 0.16	0.21	6.2
N. splendida	5	5.31 ± 0.60	8.48 ± 0.65	3.17	37.4
	10	4.50 ± 0.46	7.13 ± 0.38	2.63	36.9
	15	3.84 ± 0.23	6.37 ± 0.53	2.52	39.6
	20	3.19 ± 0.33	6.24 ± 0.53	3.05	48.9
	25	2.52 ± 0.27	5.25 ± 0.58	2.73	52.0
	28	2.26 ± 0.20	4.83 ± 0.74	2.57	53.2
	32	2.35 ± 0.17	4.09 ± 0.42	1.74	42.5
	35	2.69 ± 0.15	2.96 ± 0.25	0.27	9.2
N. bourkii	5	4.40 ± 0.42	7.89 ± 0.95	3.49	44.2
	10	4.10 ± 0.11	6.18 ± 0.48	2.08	33.6
	15	3.55 ± 0.28	5.76 ± 0.61	2.20	38.2
	20	2.97 ± 0.20	5.34 ± 0.57	2.37	44.4
	25	2.38 ± 0.29	4.28 ± 0.90	1.90	44.5
	28	2.13 ± 0.17	4.30 ± 0.97	2.17	50.5
	32	2.04 ± 0.14	3.41 ± 0.90	1.36	40.0
	35	2.23 ± 0.26	3.34 ± 0.57	1.10	33.1

α - active phase. β - rest phase.

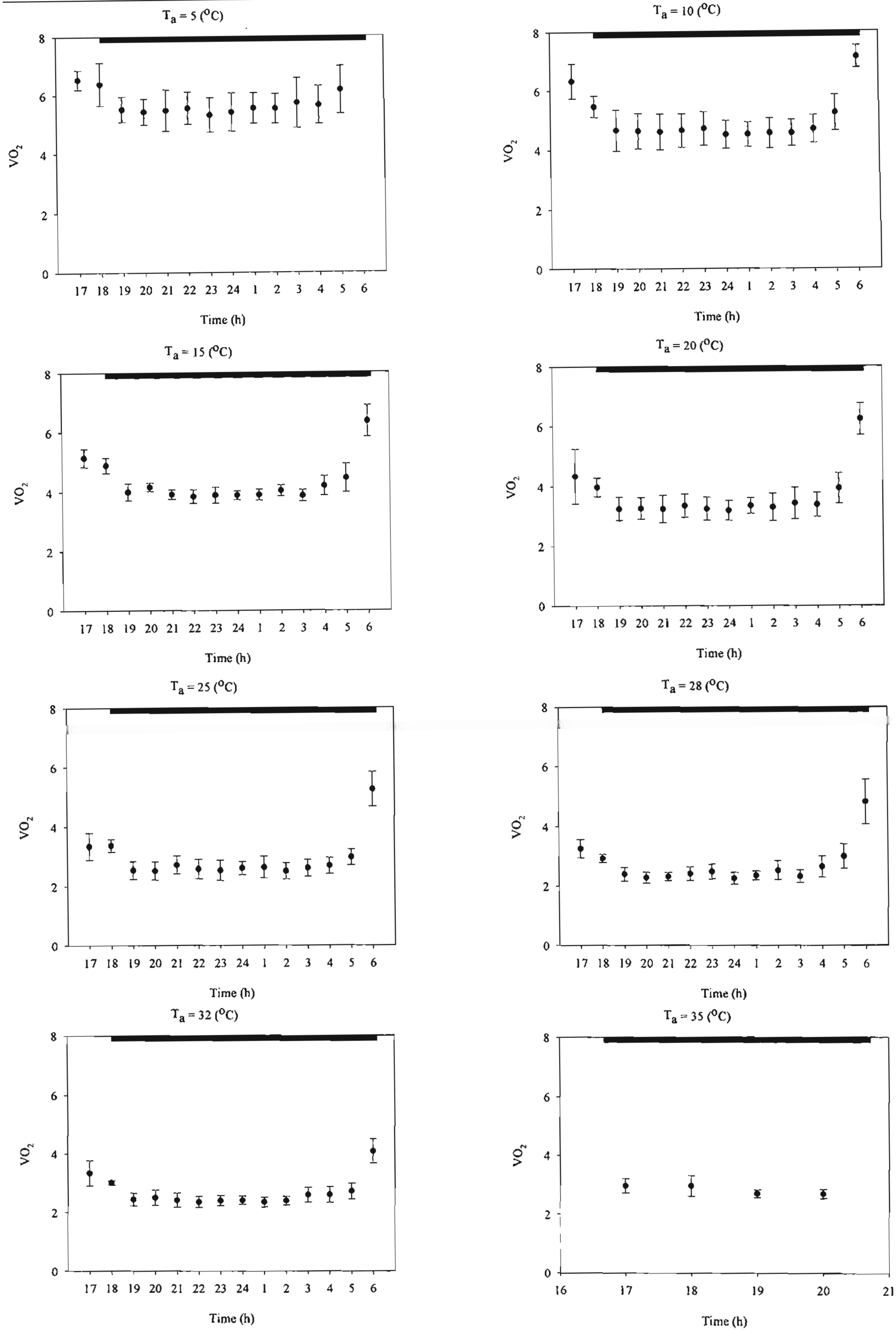


Figure 2.4 Change in oxygen consumption (VO_2, measured in ml O_2 g^{-1} h^{-1}) of *N. bourkii* with time for the various ambient temperatures (T_a) (mean ± SD, *n* = 5)

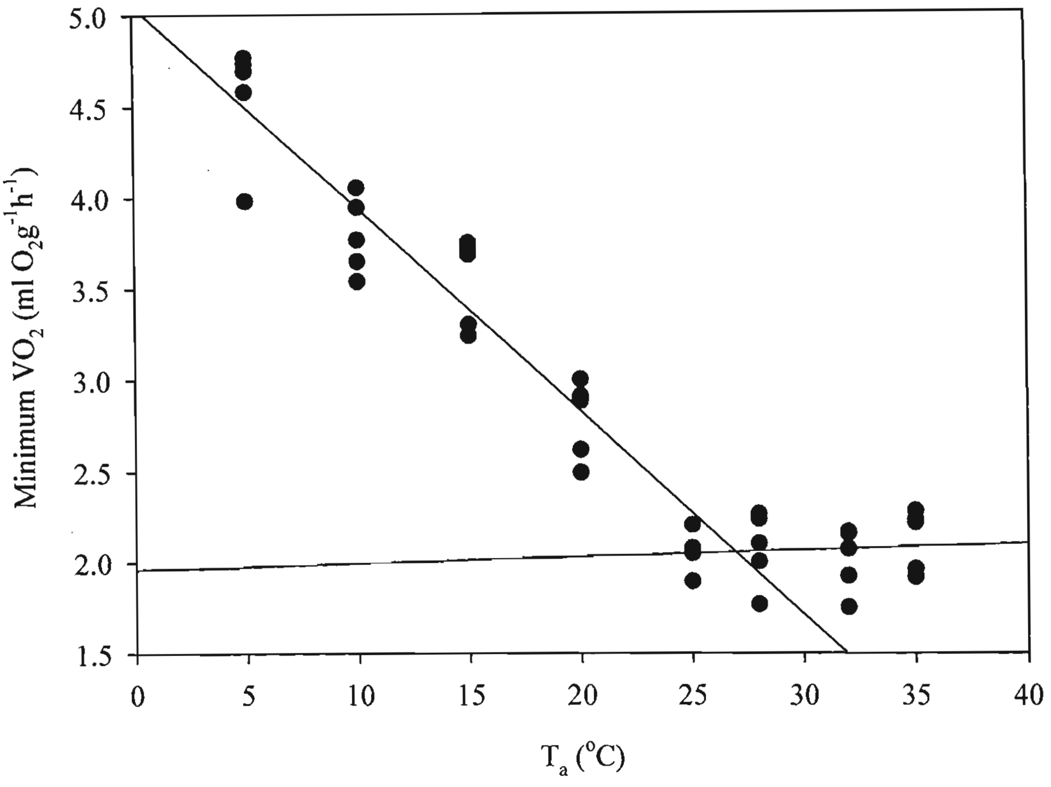


Figure 2.5 Metabolic rate as a function of air temperature in *Agapornis fischeri*, showing the piecewise linear regression analysis used to calculate the lower critical limit of thermoneutrality.

The T_{lc}s are summarised, with the equation for the regression below the T_{lc}, for all species (Table 2.4). Most species had T_{lc}s in the high twenty degree Celsius range (Figure 2.5). *Neophema elegans*, however, had a T_{lc} of 21.2 °C, which is substantially lower than all the other species. There appears to be no set pattern to the T_{lc}'s, with birds from all habitats showing similar lower critical limits.

Table2.3. Metabolic rate as a function of T_a for all study species. The equations are in the form metabolic rate (ml O_2 g^{-1} h^{-1}) = $a*T_a + b$. The number of observations (n) comprises the regression of all points below the T_{lc}. T_{lc} (°C) is the lower critical limit of thermoneutrality.

Species		a (±SE)	b	n	T_{lc} (°C)
Agapornis fischeri	$<T_{lc}$	-0.11 ± 0.41	5.05	20	27.3
Agapornis nigrigenis	$<T_{lc}$	-0.13 ± 0.04	6.23	20	30.1
Agapornis personatus	$<T_{lc}$	-0.12 ± 0.15	5.38	20	28.0
Agapornis roseicollis	$<T_{lc}$	-0.13 ± 0.13	5.41	25	27.5
Neophema elegans	$<T_{lc}$	-0.16 ± 0.07	6.06	16	21.2
Neophema pulchella	$<T_{lc}$	-0.12 ± 0.20	5.87	24	28.3
Neophema splendida	$<T_{lc}$	-0.14 ± 0.06	5.94	30	26.0
Neopsephotus bourkii	$<T_{lc}$	-0.10 ± 0.10	5.03	20	29.4

Interspecific analyses of BMR in small parrots

Basal metabolic rate (Table2.3) was calculated for each species from the respirometry data.

Table 2.4. Basal metabolic rate and body mass of study species (mean ± SD).

Species	Habitat	BMR (W)	M_b (g)
Agapornis fischeri	semi-arid	0.56 ± 0.18	49.59 ± 6.14
Agapornis nigrigenis	mesic	0.51 ± 0.16	41.37 ± 1.05
Agapornis personatus	semi-arid	0.51 ± 0.19	46.77 ± 5.01
Agapornis roseicollis	arid	0.55 ± 0.20	53.53 ± 2.85
Neophema elegans	semi-arid	0.62 ± 0.34	42.06 ± 2.25
Neophema pulchella	mesic	0.58 ± 0.12	41.90 ± 2.09
Neophema splendida	arid	0.52 ± 0.20	40.86 ± 1.25
Neopsephotus bourkii	arid	0.49 ± 0.14	42.75 ± 2.28

After constructing a phylogeny for the study species (Figure 2.6), $\log_{10}$ basal metabolic rates and $\log_{10}$ body masses were entered as tip values. PICs calculated using this phylogeny were analysed by conventional and phylogenetically independent methods (Table 2.4). Both the conventional and phylogenetically independent methods yielded no significant differences in BMR between the different habitats. There were also no significant differences between the species assemblages from Africa and Australia.

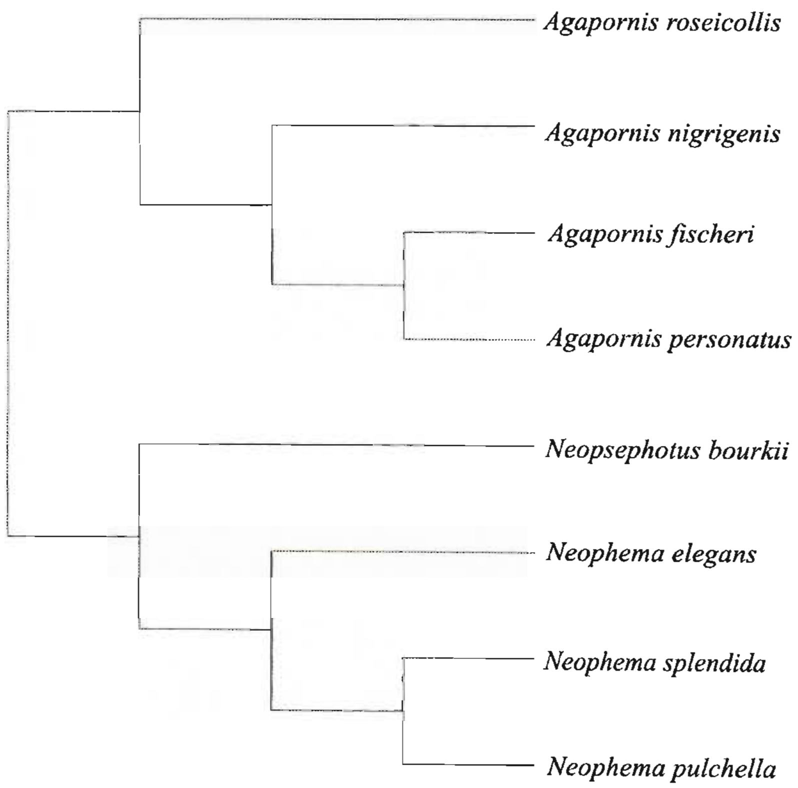


Figure 2.6 Phylogeny of the study species constructed using morphological and molecular data (Moreau 1948; Leeton et al. 1994; Williams 1996; Collar 1997; Eberhard 1998).

Table2.5. ANCOVA of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) of African (n = 4) and Australian (n = 4) parrots, as well parrots from mesic (n = 2), semi-arid (n = 3) and arid (n = 3) habitats. Critical values of the 95th percentile were gathered from conventional tables and calculated from data generated by 10 000 Monte Carlo simulations of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) evolution using Brownian motion as the null process of character change.

					Conventional tables		Brownian Gradual without bounds	
Source of variation	SS	df	MS	*F*	Critical value	*P*	Critical value	*P*
	Conventional ANCOVA						**PD***	
Among continents	0.0009	1	0.0009	0.63	5.59	>0.05	21.78	>0.05
Error	0.007	5	0.001					
Total	0.008	7	0.001					
Among habitats	0.001	2	0.001	0.59	4.73	>0.05	6.56	>0.05
Error	0.006	4	0.001					
Total	0.008	7	0.001					

*Phylogenetically independent *F*-statistic distribution

DISCUSSION

The Rosy-faced Lovebird's BMR is higher than that reported by Kendeigh et al. (1977), but consistent with that found by Bucher and Morgan (1989). However, Bucher and Morgan (1989) measured metabolic rate during the active phase and could not assume that their result was basal. The BMR of the Bourke's Parakeet was lower than that reported by Dawson (1965), but that study did not report under which phase measurements were made. Lindgren's (1973) BMR result for *N. elegans* was slightly lower than that found in this study, but he used different techniques for measurements of metabolic rate.

The results, however, give no statistical support to the idea that desert-dwelling parrots have lower basal metabolic rates than their non-desert dwelling counterparts. This supports the results of Williams et al. (1991), who showed that Australian desert-dwelling parrots (Budgerigar *Melopsittacus undulatus*, Bourke's Parakeet *Neopsephotus bourkii*, Cockatiel *Nymphicus hollandicus*, Port Lincoln Parrot *Barnardius zonarius*, Galah *Cacatua roseicapilla* and Red-tailed Cockatoo *Calyptorhynchus magnificus*) did not have reduced BMRs, or field metabolic rates, in comparison with more mesic species (Rock Parakeet *Neophema petrophilla*, Elegant Parakeet *Neophema elegans*, Rainbow Lorikeet *Trichoglossus haemtodus*, Long-billed Corella *Cacatua tenuirostris* and Sulfur-crested Cockatoo *Cacatua galerita*).

The lack of any clear distinction between desert and non-desert species has several explanations. Consider first the problem of phenotypic plasticity. Phenotypic plasticity can be explained as the ability of a genotype to exhibit a variety of phenotypes (Gabriel 2005). The range of phenotypes that result from a genotype are most often determined by the environment that a species inhabits (Gabriel et al. 2005). For example, it would be anticipated that an individual bird inhabiting a mesic habitat, and then transported to an arid habitat, would exhibit a reduction in BMR (Gabriel 2005; Gabriel et al. 2005). One hypothesised cause of this reduction in BMR is the reduction in the size and mass of certain tissues in the body (Konarzewski & Diamond 1995; Piersma et al. 1996; Battley et al. 2000). The heart, kidneys, brain and intestine have been shown to contribute disproportionately to metabolic rate, so a reduction in the size and number of these tissues would lead to a lower BMR (Daan et al. 1990). Recent work by McKechnie et al. (2006) has shown that the BMR of captive-bred birds scales at a different exponent to that of wild-caught birds. All the birds used in this experiment were captive-bred, thus raising a question as to the validity of the finding. However, the effect of captive breeding on many species is not yet known, and the relationship between the BMR's of captive-bred and wild-caught parrots is uncertain.

Another possible explanation for the lack of differences between birds from such different habitats is that the species living in the desert environments may use other methods of energy conservation in order to survive in these harsh conditions. The use of thermal refugia is a well known phenomenon that reduces the heat load of deserticolous birds during periods of high T_a (Wolf 2000). The reduction in heat load of these birds has numerous positive consequences that help these species to survive habitat extremes. First, metabolic rate is reduced, as there is a reduced need to thermoregulate, due to reduced T_as. And second, as a result of this reduction in thermoregulatory requirements, there is a reduction in the pulmonary water loss normally associated with thermoregulatory processes such as gular fluttering. The use of thermal refugia usually takes the form of a movement by the bird from a sunlit area to an area that is shaded, but in extreme cases the bird may also make use of the burrows of other animals, thus reducing the T_a even further (Williams et al. 1999). Associated with the use of these thermal refugia is the suspension of activity during these periods, thus also reducing the energy expenditure of the bird. Behavioural adaptations of this type may allow a species to maintain BMR at levels equal to a similar sized individual from a more mesic environment. However, very little is known about the behavioural responses of the study species to extremes of environment.

The lack of differences between desert and non-desert dwelling parrots can equally be explained by the idea that birds do not need to reduce BMR because they have higher mass-specific metabolic rates than mammals, and a subsequently higher body temperature. These higher body temperatures allow them to offload heat down a strong temperature gradient with greater efficiency than mammals, thus reducing energy expenditure on cooling mechanisms. This hypothesis allows for the measured differences between desert and non-desert birds (Tieleman & Williams 2000), in that these adaptations may have evolved in response to food shortages, or extremes of ambient temperature that put a bird under extreme thermal stress. If this is true then Maclean's (1996) statement that "what seems adaptive in birds to the desert environment is in fact intrinsic to the avian condition" may indeed hold an element of truth. Maclean's (1996) standpoint does not, however, explain why Tieleman and Williams (2000) found significant differences between desert and non-desert bird species in terms of BMR. Perhaps the true nature of desert bird BMR patterns incorporates both these ideas. When a bird species moves into a desert environment, perhaps it is "pre-adapted" to deal with the harsh conditions. But over time adaptations may evolve that allow a species to survive better in the harsh conditions. The combination of the "pre-adapted hypothesis" (Maclean 1996), and the "post arrival adaptation hypothesis" (Tieleman & Williams 2000) would help to explain why we find some bird species in deserts that have apparently developed metabolic adaptations, while other species have apparently not developed such adaptations.

It would be of interest to expand this analysis to include more species, over a wider range of body mass, and to include a wider range of habitat types. The effect of captivity on BMR, as well as, the unknown differences between captive-bred and wild caught parrot BMRs need to be quantified. The lack of differences in BMR between parrots from varying habitats, although supported by previous studies (Williams et al. 1991), raises questions as to the mechanism of survival employed by birds in extreme environments.

It is noted that all measurements in this study were made on birds that had been acclimated to 12L:12D, as an arbitrary or neutral acclimation regime. Since seasonal phenotypic plasticity is known to occur in mammals (Lovegrove 2005), future studies must examine this role in birds by measuring the reaction norm (Stearns 1992), that is, the range of BMR that can be measured at acclimation extremes. Examples of this include high T_a and long photoperiod, versus low T_a and short photoperiod.

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LITERATURE CITED

BARTHOLOMEW, G. A. & CADE, T. J. 1963. The water economy of land birds. *Auk* **80**: 504-539.

BATTLEY, P. F., PIERSMA, T., DIETZ, M. W., TANG, S., DEKINGA, A., & HULSMAN, K. 2000. Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proceedings of the Royal Society of London B* **267**: 191-195.

BUCHER, T. L. & MORGAN, K. R. 1989. The effect of ambient temperature on the relationship between ventilation and metabolism in a small parrot (*Agapornis roseicollis*). *Journal of Comparative Physiology* **159**: 561-567.

CHEVERUD, J. M., DOW, M. M., & LEUTENEGGER, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* **39**: 1335-1351.

COLLAR, N. J. 1997. Family Psittacidae (Parrots). In: *Handbook of the Birds of the World. Vol. 4. Sandgrouse to Cuckoos,* (eds.) J. del Hoyo, A. Elliot, & J. Sargatal. Lynx Edicions, Barcelona.

DAAN, S., MASMAN, D., & GROENEWOLD, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *American Journal of Physiology* **259**: R333-R340.

DAWSON, W. R. 1965. Evaporative water losses of some Australian parrots. *Auk* **82**: 106-108.

DAWSON, W. R. & BENNETT, A. F. 1973. Roles of metabolic level and temperature regulation in the adjustment of Western Plumed Pigeons (*Lophophaps ferruginea*) to desert conditions. *Comparative Biochemistry and Physiology A* **44**: 249-266.

DOWNS, C. T. & SYMES, C. T. 2004. Snag dynamics and forest structure in Afromontane forests in KwaZulu-Natal, South Africa: implications for the conservation of cavity-netsing avifauna. *South African Journal of Botany* **70**: 265-276.

EBERHARD, J. 2002. Cavity adoption and the evolution of coloniality in cavity-nesting birds. *The Condor* **104**: 240-247.

EBERHARD, J. R. 1998. Evolution of nest-building behaviour in *Agapornis* parrots. *Auk* **115**: 455-464.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125**: 1-15.

FISHER, C. D., LINDGREN, E., & DAWSON, W. R. 1972. Drinking patterns and behavior of Australian desert birds in relation to their ecology and abundance. *The Condor* **74**: 111-136.

FORSHAW, J. M. 1977. *Parrots of the World.* T.F.H. Publications, Neptune City, N.J.

GABRIEL, W. 2005. How stress selects for reversible phenotypic plasticity. *Journal of Evolutionary Biology* **18**: 873-883.

GABRIEL, W., LUTTBEG, B., SIH, A., & TOLLRIAN, R. 2005. Environmental tolerance, heterogeneity, and the evolution of reversible plastic responses. *American Naturalist* **166**: 339-353.

GARLAND, T., DICKERMAN, A. W., JANIS, C. M., & JONES, J. A. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**: 265-292.

GARLAND, T., HARVEY, P. H., & IVES, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18-32.

GIBBS, A. G. 2002. Water balance in desert *Drosophila*: lessons from non-charismatic microfauna. *Comparative Biochemistry and Physiology A* **133**: 781-789.

GOLDSTEIN, D. L. & NAGY, K. A. 1985. Resource utilization by desert quail: time and energy, food and water. *Ecology* **66**: 378-387.

HARVEY, P. H. & PAGEL, M. D. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

HOMBERGER, D. G. 1994. The adaptive radiation of the ecology, bill structure, and feeding mechanism of the Australian Cockatoos as a model for the evolution of seed predation in Psittaciformes. *Journal fur Ornithologie* **135**: 435-

JUNIPER, T. & PARR, M. 1998. *Parrots: a guide to the parrots of the world.* Pica Press, Sussex.

KENDEIGH, S. C., DOL'NIK, V. R., and GAVRILOV, V. M. 1977. Avian energetics. In: *Granivorous birds in ecosystems,* (eds.) J. Pinowski & S. C. Kendeigh. Cambridge University Press, Cambridge.

KONARZEWSKI, M. & DIAMOND, J. 1995. Evolution of basal metabolic rate and organ masses in laboratory mice. *Evolution* **49**: 1239-1248.

LEETON, P. R., CHRISTIDIS, L., WESTERMAN, M., & BOLES, W. E. 1994. Molecular phylogenetic affinities of the Night Parrot (*Geopsittacis occidentalis*) and the Ground Parrot (*Pezoporus wallicus*). *The Auk* **111**: 833-843.

LINDGREN, E. 1973. *Studies in the ecology and physiology of three species of grass-parrots (Neophema. Aves: Psittacidae)*. PhD thesis. University of Western Australia

LOUW, G. N. & SEELY, M. 1982. *Ecology of desert organisms*. Longman, London.

LOVEGROVE, B. G. 2005. Seasonal thermoregulatory responses in mammals. *Journal of Comparative Physiology B* **175**: 231-247.

MACLEAN, G. L. 1996. *Ecophysiology of Desert Birds.* Springer-Verlag, Berlin Heidelberg.

MCKECHNIE, A. E., FRECKLETON, R. P., & JETZ, W. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society of London B* **273**: 931-937.

MEIGS, P. 1953. *Reviews of Research on Arid Zone Hydrology.* UNESCO, Paris.

MOREAU, R. E. 1948. Aspects of the evolution in the parrot genus *Agapornis. Ibis* **90**: 206-239.

PAGEL, M. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* **156**: 431-442.

PIERSMA, T., BRUINZEEL, L., DRENT, R., KERSTEN, M., VAN DER MEER, J., & WIERSMA, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* **69**: 191-217.

R DEVELOPMENT CORE TEAM 2006. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

STEARNS, S. C. 1992. *The evolution of life histories.* Oxford University Press, Oxford.

THOMAS, D. H. & MACLEAN, G. L. 1981. Comparison of physiological and behavioural thermoregulation and osmoregulation in two sympatric sandgrouse species (Aves: Pteroclididae). *Journal of Arid Environments* **4**: 335-358.

THORNTHWAITE, C. W. 1948. An approach toward a rational classification of climate. *Geographical Reviews* **38**: 55-94.

TIELEMAN, B. I. & WILLIAMS, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**: 461-479.

TIELEMAN, B. I., WILLIAMS, J. B., & BLOOMER, P. 2003. Adaptation of metabolic rate and evaporative water loss along an aridity gradient. *Proceedings of the Royal Society of London* **270**: 207-214.

TROST, C. H. 1972. Adaptations of horned larks (*Eremophila alpestris*) to hot environments. *Auk* **89**: 506-527.

WIKELSKI, M., SPINNEY, L., SCHELSKY, W., SCHEUERLEIN, A., & GWINNER, E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B* **270**: 2383-2388.

WILLIAMS, J. B. 1996. A phylogenetic perspective of evaporative water loss in birds. *The Auk* **113**: 457-472.

WILLIAMS, J. B., TIELEMAN, B. I., & SHOBRAK, M. 1999. Lizard burrows provide thermal refugia for larks in the Arabian desert. *Condor* **101**: 714-717.

WILLIAMS, J. B., WITHERS, P. C., BRADSHAW, S. D., & NAGY, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Australian Journal of Zoology* **39**: 131-142.

WITHERS, P. C. 1977. Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* **42**: 120-123.

WITHERS, P. C. & WILLIAMS, J. B. 1990. Metabolic and respiratory physiology of an arid-adapted Australasian bird, the Spinifex pigeon. *Condor* **92**: 961-969.

WOLF, B. O. 2000. Global warming and avian occupancy of hot deserts: a physiological and behavioral perspective. *Revista Chilena de Historia Natural* **75**: 387-392.

CHAPTER THREE

AN INTERSPECIFIC ANALYSIS OF BASAL METABOLIC RATE IN CAPTIVE-RAISED AND WILD-CAUGHT PARROTS

INTRODUCTION

Physiological diversity in endotherms arises as a result of several sources of phenotypic variation (McKechnie et al. 2006). Analyses of endotherm metabolic diversity have primarily focused on the allometric scaling of metabolic traits with body mass (M_b) and/or the adaptation of metabolism to biotic and abiotic environmental characteristics (Lasiewski & Dawson 1967; McNab 1986; Lovegrove 2000; Tieleman & Williams 2000a; Mueller & Diamond 2001; White & Seymour 2003; Lovegrove 2003; Wikelski et al. 2003; McKechnie et al. 2006). Recent work by a number of authors, however, shows an increasing interest in other sources of metabolic variation, with many studies now focusing on the role of phenotypic plasticity in the diversity of physiological responses shown by endotherms (Piersma & Drent 2003; McKechnie et al. 2006). Phenotypic plasticity may incorporate short-term, reversible changes within an individual (phenotypic flexibility), and/or irreversible changes resulting from developmental processes (developmental plasticity) (Piersma & Drent 2003). Lovegrove (2005) showed seasonal phenotypic flexibility in the basal metabolic rate (BMR) of numerous mammal species, with the direction of these metabolic adjustments varying with M_b. There is also increasing evidence that birds exhibit considerable phenotypic flexibility in metabolic rate, with short-term adjustments in BMR having been found in many bird species (Piersma et al. 1995; Tieleman et al. 2003).

BMR is a baseline metabolic parameter that represents maintenance energy demand when there are no increases in metabolism associated with digestion, thermoregulation, activity, reproduction, growth or circadian rhythm (McNab 1997). As such BMR is often used to compare species of varying size, and from varying zoogeographic regions (Weathers 1979; Lovegrove 2000; Tieleman & Williams 2000a; Lovegrove 2003; Cruz-Neto & Bozinovic 2004; Hulbert & Else 2004; Lovegrove 2005). Comparative analyses of avian basal metabolic rates most commonly examine the variation in basal metabolic rates between birds of differing taxonomic affiliation, M_b, or birds from different habitats (Weathers 1979; Aschoff 1981; Tieleman et al. 2003; McKechnie & Wolf 2004a; McKechnie & Wolf 2004b). With the recent realisation that phenotypic flexibility may complicate the identification of metabolic adaptation, some authors have employed experimental designs referred to as common-garden experiments (Wikelski et al. 2003; McKechnie et al. 2006). These experiments control for developmental plasticity by raising birds from distinct populations under identical conditions before any comparison of metabolic or behavioural parameters are made (Wikelski et al. 2003).

A recent study by McKechnie et al. (2006) has shown that the scaling exponent relating BMR to M_b in captive-raised birds was significantly shallower than in wild-caught birds. Avian data sets from the literature included estimates of BMR for both captive-raised and wild-caught birds, but in the past these data sets had been pooled (McKechnie et al. 2006). McKechnie et al. (2006) managed to detect the signal of phenotypic plasticity in these data sets, thus calling into question any previous study that merged these data sets for interspecific analyses of variation in BMR. The disparity between captive-raised and wild-caught birds questions the validity of this study, and so an interspecific analysis of all available parrot BMR data should elucidate the accuracy of the data produced in this study. I hypothesised that parrots will show the same disparity in the scaling exponent of BMR between captive-raised and wild-caught species, as was detected by McKechnie et al. (2006). I further hypothesised that the parrots will have higher BMRs than predicted by body size (Bennett & Harvey 1987; McNab 1988; Williams et al. 1991).

METHODS

Basal Metabolic Rate Data

I obtained BMR (Watts) and M_b (grams) data for 242 avian species from the literature, this study, and unpublished data from M. R. Perrin (Appendix one). Metabolic rates were only included if they were measured during the rest phase of the circadian cycle at thermoneutral air temperatures in resting individuals that could be assumed to be postabsorptive (McKechnie & Wolf 2004b). However, no attempt was made to control for photoperiod in the data set. Data were included irrespective of sample size, as this nearly doubled the size of the data set, although some of the data therefore represent the means of only one or two individuals. However, the BMR of an individual is equally likely to be above or below the population mean, and therefore these data should not significantly affect the conclusions that can be drawn (McKechnie et al. 2006). All M_b and BMR data were log-transformed prior to analysis. Original sources were consulted in order to classify each datum as captive-raised (birds that were bred in captivity, or had spent most of their lives in captivity) or wild-caught (birds obtained from wild populations, and kept in captivity for short periods). Several species were excluded due to their large M_b as they were only represented in the wild-caught category.

Data Analyses

It has been argued that the comparison of data across species by conventional means violates the statistical assumption of independence by virtue of the relatedness of these species in a phylogenetic framework (Felsenstein 1985; Cheverud et al. 1985; Harvey & Pagel 1991). I therefore constructed a phylogeny (Appendix two) based primarily on Sibley & Ahlquist's (1990) DNA-hybridization data, using the phylogenies in Moreau (1948), Reynolds & Lee (1996), Miyaki et al. (1998), Racheli (1999), Massa et al. (2000), Tieleman & Williams (2000b), McKechnie (2001), Schleucher (2002), Tieleman et al. (2002) and McKechnie & Wolf (2004b). PDTREE was used to create the phylogeny and calculate the Phylogenetically independent contrasts (PICs) (Garland et al. 1992). In order to adequately standardise contrasts the phylogeny branch lengths were transformed using the Nee method (Garland et al. 1992). PDSINGLE was used to calculate conventional ANCOVA for observed $\log_{10}$ BMR of captive-raised and wild-caught species (Garland et al. 1992; Garland et al. 1999; Garland & Ives 2000). The observed F-value from the conventional ANCOVA was compared with the critical 95th percentile F-values from conventional tables. It was also compared with 95th percentile critical F-values from null F-distributions generated from 10 000 Monte Carlo simulations of BMR (with M_b as co-variate) evolution along the bird phylogeny using PDSIMUL and PDANOVA (Garland et al. 1993). The simulations (gradual without bounds) assumed Brownian motion as the null process of character change (Garland et al. 1993). I first verified the differences between captive-raised and wild-caught birds, as shown by McKechnie et al. (2006). I then tested for differences between parrots and all other birds. Finally, I tested for differences between captive-raised and wild-caught parrots using a reduced phylogeny for the parrots alone (Appendix three).

RESULTS

Using conventional generalised least squares regression, calculated in PDSINGLE, the overall relationship between BMR (W) and M_b (g) was best described by the linear regression $\log_{10}\text{BMR} = 0.629\log_{10}M_b - 1.370$. I then tested for differences in BMR between captive-raised ($N = 105$) and wild-caught ($N = 137$) bird species. Population origin had a significant affect on the slope of the relationship between M_b and BMR (Figure 3.1). Wild-caught birds showed a steeper scaling coefficient (0.657) than captive-raised birds (0.584). Conventional analysis of variance revealed significant differences between the scaling coefficients of the two groups, as well as between the two groups in general (Table 3.1). However, the phylogenetically dependent F-distribution yielded a critical value that was larger than the calculated F ratio. The conventional analysis, therefore, yielded significant differences between captive-raised and wild-caught birds, whereas the phylogenetically dependent analysis found non-significant differences between the two groups (Table 3.1).

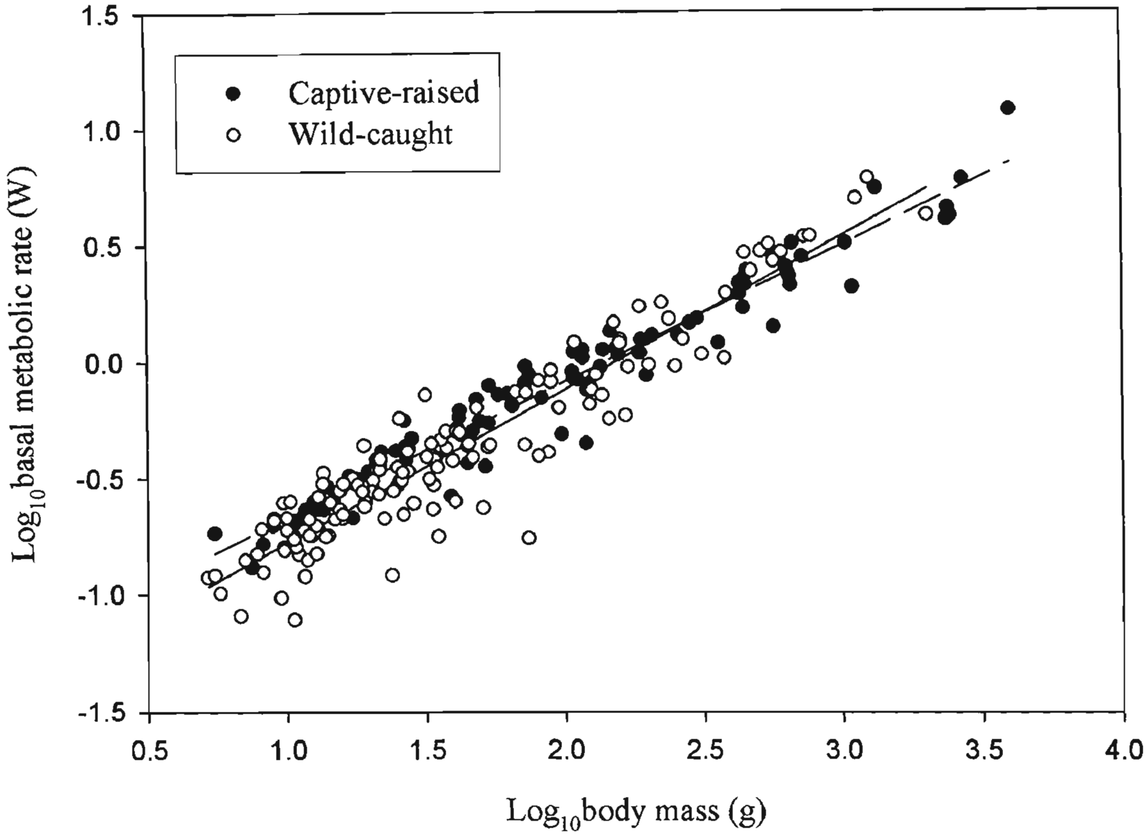

Figure 3.1. The scaling relationship between basal metabolic rate (BMR) and body mass (M_b) differs between birds from wild-caught and captive-raised populations. The solid line is the scaling relationship [$\log_{10}BMR = 0.657\log_{10}M_b - 1.435$ (N = 137)] for wild-caught birds. The dashed line is the corresponding relationship for captive-raised birds [$\log_{10}BMR = 0.584\log_{10}M_b - 1.256$ (N = 105)].

The conventional test for differences in BMR between parrots (N = 20) and all other birds (N = 222) showed a significant difference between the two groups (Table 3.2). The slopes of the two regression lines were, however, not significantly different form each other, with parrots having a scaling coefficient of 0.623, and all the other birds having a scaling coefficient of 0.626 (Figure 3.2). However, a Levene's median-ratio test for differences in

Table 3.1. ANCOVA of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) of captive-raised (n = 105) and wild-caught (n = 137) birds. Critical values of the 95th percentile were gathered from conventional tables and calculated from data generated by 10 000 Monte Carlo simulations of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) evolution using Brownian motion as the null process of character change.

					Conventional tables		Brownian Gradual without bounds	
Source of variation	SS	df	MS	*F*	Critical value	*P*	Critical value	*P*
	Conventional ANCOVA						**PD***	
Among groups	0.15	1	0.15	10.55	3.87	<0.05	12.70	>0.05
Error	3.49	239	0.01					
Total	43.50	241	0.18					
Among slopes	0.12	1	0.12	8.81	3.87	<0.05	9.46	>0.05
Error	3.36	238	0.01					

*Phylogenetically independent *F*-statistic distribution

variability among subsets revealed a highly significant difference in the variances of the two groups. The phylogenetically dependent *F*-distribution yielded a critical *F* value that far exceeded the observed *F*-ratio (Table 3.2). The conventional analysis therefore shows

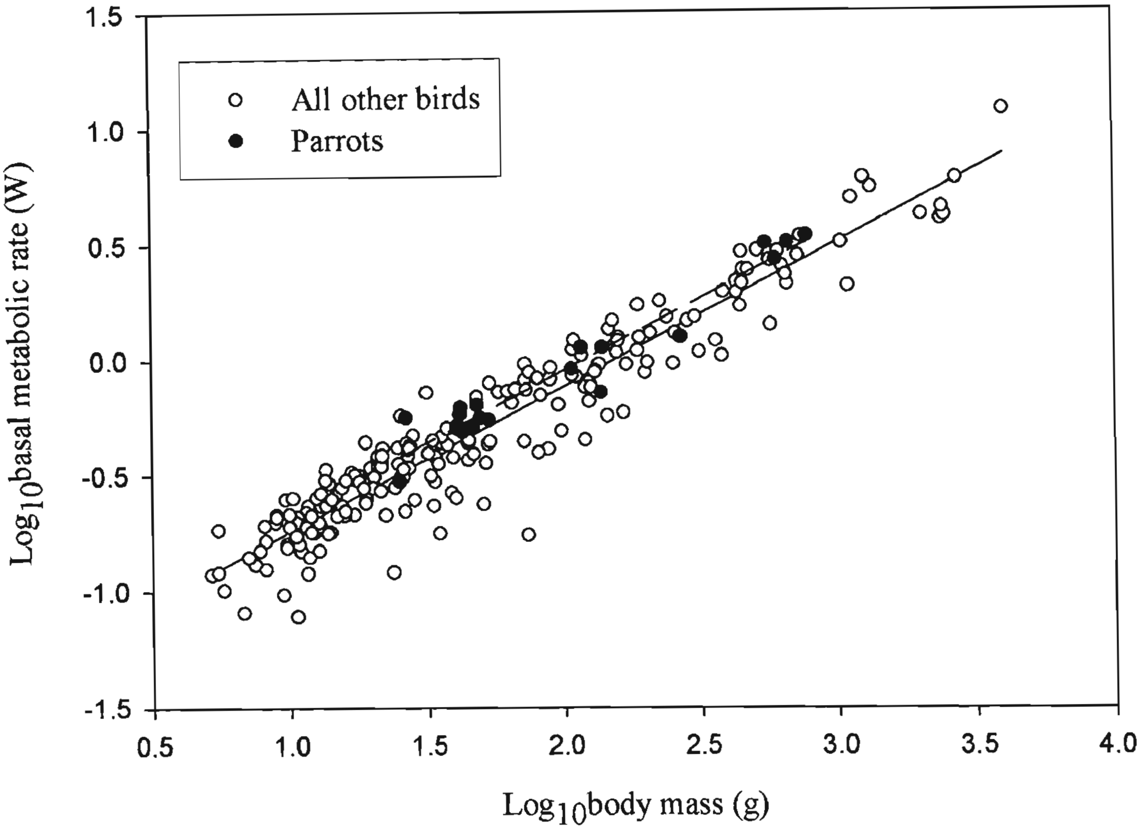

Figure 3.2. The scaling relationship between basal metabolic rate (BMR) and body mass (M_b) differs between parrots and all other birds. The solid line is the scaling relationship [$\log_{10}BMR = 0.626\log_{10}M_b - 1.369$ (N = 222)] for all other birds. The dashed line is the corresponding relationship for parrots [$\log_{10}BMR = 0.623\log_{10}M_b - 1.297$ (N = 20)].

the two groups as having regressions that are parallel but significantly different from one another. However the Levene's test shows heterogeneous variances, thus disallowing comparison of the two groups due to the violation of one of the assumptions of any statistical test. The phylogenetically dependent analysis reveals no significant differences between the two groups.

Table 3.2. ANCOVA of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) of parrots (n = 20) and all other birds (n = 222). Critical values of the 95th percentile were gathered from conventional tables and calculated from data generated by 10 000 Monte Carlo simulations of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) evolution using Brownian motion as the null process of character change.

							Brownian	
					Conventional tables		Gradual without bounds	
Source of variation	SS	df	MS	*F*	Critical value	*P*	Critical value	*P*
Conventional ANCOVA							**PD***	
Among groups	0.08	1	0.08	5.84	3.87	<0.05	82.60	>0.05
Error	3.55	239	0.01					
Total	43.54	241	0.18					
Among slopes	0.00001	1	0.00001	0.0009	3.87	>0.05	4.58	>0.05
Error	3.55	238	0.01					

*Phylogenetically independent *F*-statistic distribution

The test for differences in BMR between captive-raised (N=15) and wild-caught (N=5) parrots revealed no significant differences between the two groups. The scaling

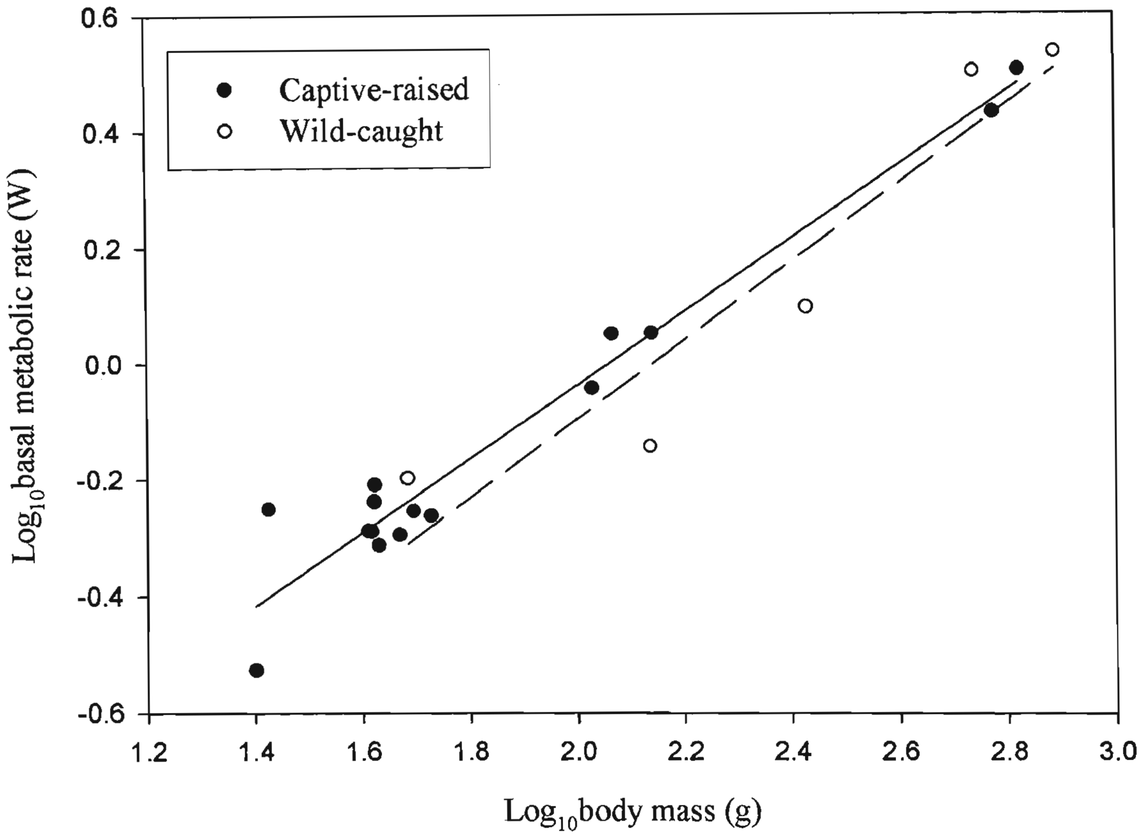

Figure 3.3. The scaling relationship between basal metabolic rate (BMR) and body mass (M_b) does not differ significantly between parrots from wild-caught and captive-raised populations. The solid line is the scaling relationship [$\log_{10}\mathrm{BMR} = 0.632\log_{10}M_b - 1.303$ (N = 15)] for captive-raised parrots. The dashed line is the corresponding relationship for wild-caught parrots [$\log_{10}\mathrm{BMR} = 0.684\log_{10}M_b - 1.443$ (N = 5)].

coefficient for captive-raised parrots (0.632) was not significantly different from the scaling exponent for wild-caught parrots (0.684) (Figure 3.3). The phylogenetically dependent *F*-distribution revealed no significant differences (Table 3.3).

Table 3.3. ANCOVA of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) of captive-raised (n = 15) and wild-caught (n = 5) parrots. Critical values of the 95th percentile were gathered from conventional tables and calculated from data generated by 10 000 Monte Carlo simulations of $\log_{10}$BMR (with $\log_{10}$body mass as co-variate) evolution using Brownian motion as the null process of character change.

							Brownian	
					Conventional tables		Gradual without bounds	
Source of variation	SS	df	MS	*F*	Critical value	*P*	Critical value	*P*
	Conventional ANCOVA						**PD***	
Among groups	0.08	1	0.08	0.26	4.54	>0.05	10.19	>0.05
Error	0.09	16	0.005					
Total	1.88	18	0.10					
Among slopes	0.001	1	0.001	0.31	4.54	>0.05	7.05	>0.05
Error	0.09	15	0.006					

*Phylogenetically independent *F*-statistic distribution

DISCUSSION

The historical origins of birds have a significant effect on their BMR, and reveal a signal of phenotypic plasticity in avian BMR data sets (McKechnie et al. 2006). The differences in scaling between captive-raised and wild-caught birds indicate that the origins of a population of birds must be taken into account when testing for metabolic adaptation (McKechnie et al. 2006). Tests for metabolic divergences in the BMR of multiple taxa, or tests for adaptation in single taxa, may be misled by the differences between captive-raised and wild-caught birds (McKechnie et al. 2006). Many studies have made the assumption that the BMR of captive-raised individuals is representative of the BMR of wild individuals (McNab 2001; Schleucher & Withers 2002). Only a few studies have examined the effects of captivity on the BMR of birds, with perhaps the best known being that by Weathers et al. (1983), who found similar BMRs in recently caught Apapanes (*Himatione sanguinea*) and Apapanes that had been in captivity for a year. Very few BMR estimates are available for wild-caught and captive-raised populations of a species, but for the Speckled Mousebird (*Colius striatus*) such data does exist. McKechnie & Lovegrove (2001a) found that wild-caught Speckled Mousebirds had BMR's that were approximately 75% of the BMR's of second- and third-generation captive-raised individuals measured by Bartholomew & Trost (1970).

Conventional and phylogenetically-independent analyses of interspecific and intraspecific metabolic variation have often assumed that this variation is due to adaptation through natural selection (Lovegrove 2000; Merola-Zwartjes & Ligon 2000; Lovegrove 2003). This is an invalid assumption for avian BMRs, as they are affected by phenotypic plasticity (McKechnie et al. 2006). McKechnie et al. (2006) suggest the use of data from wild-caught birds only, when attempting to correlate avian BMR with ecological factors. While this may reduce the effect of phenotypic plasticity, caution must still be taken that phenotypic flexibility is not mistaken for metabolic adaptation. The use of carefully controlled common garden experiments can help to reduce developmental plasticity by virtue of their design, thus allowing a clearer comparison of any interspecific or intraspecific differences that may be present (Wikelski et al. 2003). Tieleman et al. (2003) suggested another approach and tested for phenotypic flexibility in BMR for numerous lark species from arid and mesic habitats. Larks from arid habitats did not show greater BMR flexibility than larks from mesic habitats, as had been predicted (Tieleman et al. 2003). Ambrose & Bradshaw (1988), however, showed a 20% reduction in the summer BMR of White-browed Scrubwrens (*Sericornis frontalis*) inhabiting semi-arid habitats, while another population living in more mesic habitat did not show this reduction in summer BMR. These data confirm the potential for seasonal phenotypic plasticity in birds that may be obscuring the pattern that was expected.

McKechnie et al. (2006) assumed that the differences in BMR between wild-caught and captive-raised birds reflected phenotypic adjustments, and not genotypic divergence due to selective breeding. This assumption is due to the artificial selection that many captive populations are subject to. Artificial selection pressure arises in order to increase breeding success and/or for the selection of specific plumage colour or other traits. However, selection pressure over only a few generations is unlikely to cause significant changes in the metabolic traits of a species. It can therefore be assumed that phenotypic adjustments are due to phenotypic flexibility and/or developmental plasticity; but we cannot distinguish between these two types of phenotypic plasticity in this analysis. However, it has been shown that avian BMR can be adjusted over short time-scales of days to weeks (Lindström 1997; Battley et al. 2001; Tieleman et al. 2003), and many of the species included in this analysis spent several weeks in captivity prior to BMR measurements (McKechnie & Lovegrove 2001b; 2003). This suggests that differences between captive-raised and wild-caught birds are partly due to developmental effects ((McKechnie et al. 2006).

Conventional analysis of variance found that parrots had significantly higher BMRs than predicted by M_b when compared with all other birds in this analysis. This confirms the conclusions of Williams et al. (1991), who found that Australian parrots had higher BMRs than those predicted by M_b. The general relationship of higher BMRs in parrots, when compared to other birds, has also been reported by Bennett & Harvey (1987) and McNab (1988). However, the phylogenetically dependent analysis yielded non-significant differences between parrots and all other birds. Levene's median-ratio test for differences in variability among subsets revealed significant differences between the variances of the two groups, which may partially explain the reason why the phylogenetically dependent F_{crit} was so large, and therefore found non-significant differences. Since the variances were heterogeneous, a test for differences between the two groups violates one of the principle assumptions of any statistical test. Possible reasons for this heterogeneity in variances are many and varied, however, the unequal sample sizes of the two groups may be a contributing factor. Also, the parrot group includes birds of a limited M_b range, whereas the other birds in this analysis include a large range of body masses. The first test of this study impacts on this test in an important way, since 15 of the 20 parrots in this analysis were captive-raised. The high proportion of captive-raised parrots may have elevated the parrots, as a group, above the other birds. Captive-raised parrots are, furthermore, exposed to greater artificial selective pressures than other bird groups due to their bright, colourful plumage, and their much extended history in captivity. As with the first test, it is recommended that future attempts to distinguish differences in metabolic traits between parrots and all other birds, focus on wild-caught population data (McKechnie et al. 2006). More wild-caught parrot BMR data, of a greater M_b range, is required before any definitive conclusions can be made about the BMR differences between parrots and all other birds.

The third test for differences between captive-raised and wild-caught parrots revealed non significant differences between the two groups, whether using conventional or phylogenetically independent analyses. This is surprising considering the relationship between captive-raised and wild-caught birds found by McKechnie et al. (2006). Their findings led me to expect significant differences between the different parrot groups. And, as argued above, parrots have an extended history of captivity, which led to the assumption that they would have experienced much more artificial selection than other bird groups. The lack of differences in BMR between the wild-caught and captive-raised parrots may be explained by the small sample sizes that were used in this analysis, and as argued above, more BMR data may be necessary to elucidate the presence or absence of these differences. However, there may indeed be no differences in BMR between captive-raised and wild-caught parrots. If this lack of difference is legitimate, then the conclusions drawn in Chapter 2 may indeed be valid.

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LITERATURE CITED

AMBROSE, S. J. & BRADSHAW, S. D. 1988. Seasonal changes in standard metabolic rates in the white-browed scrubwren *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. *Comparative Biochemistry and Physiology* **89A**: 79-83.

ASCHOFF, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comparative Biochemistry and Physiology A* **69**: 611-619.

BARTHOLOMEW, G. A. & TROST, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* **72**: 141-146.

BATTLEY, P. F., DEKINGA, A., DIETZ, M. W., PIERSMA, T., TANG, S., & HULSMAN, K. 2001. Basal metabolic rate declines during long-distance migratory flight in great knots. *Condor* **103**: 838-845.

BENNETT, P. M. & HARVEY, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *Journal of Zoology London* **213**: 327-363.

CHEVERUD, J. M., DOW, M. M., & LEUTENEGGER, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* **39**: 1335-1351.

CRUZ-NETO, A. P. & BOZINOVIC, F. 2004. The relationship between diet quality and basal metabolic rate in endotherms: insights from intraspecific analysis. *Physiological and Biochemical Zoology* **77**: 877-889.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125**: 1-15.

GARLAND, T., DICKERMAN, A. W., JANIS, C. M., & JONES, J. A. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**: 265-292.

GARLAND, T., HARVEY, P. H., & IVES, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18-32.

GARLAND, T. & IVES, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *The American Naturalist* **155**: 346-364.

GARLAND, T., MIDFORD, P. E., & IVES, A. R. 1999. An introduction to Phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *American Zoologist* **39**: 374-388.

HARVEY, P. H. & PAGEL, M. D. 1991. *The comparative method in evolutionary biology.* Oxford University Press, Oxford.

HULBERT, A. J. & ELSE, P. L. 2004. Basal metabolic rate: history, composition, regulation, and usefulness. *Physiological and Biochemical Zoology* **77**: 869-876.

LASIEWSKI, R. C. & DAWSON, W. R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **69**: 13-23.

LINDSTRÖM, Å. 1997. Basal metabolic rates of migrating waders in the Eurasian Arctic. *Journal of Avian Biology* **28**: 87-92.

LOVEGROVE, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *The American Naturalist* **156**: 201-219.

LOVEGROVE, B. G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B* **173**: 87-112.

LOVEGROVE, B. G. 2005. Seasonal thermoregulatory responses in mammals. *Journal of Comparative Physiology B* **175**: 231-247.

MASSA, R., SARÀ, M., PIAZZA, M., GAETANO, C. D., RANDAZZO, M., & COGNETTI, G. 2000. A molecular approach to the taxonomy and biogeography of African parrots. *Italian Journal of Zoology* **67**: 313-317.

MCKECHNIE, A. E. 2001. *Patterns, mechanisms and evolution of avian facultative hypothermic responses: a southern African perspective.* PhD thesis. University of Natal

MCKECHNIE, A. E., FRECKLETON, R. P., & JETZ, W. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society of London B* **273**: 931-937.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2001a. Heterothermic responses in the speckled mousebird (*Colius striatus*). *Journal of Comparative Physiology B* **171**: 507-518.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2001b. Thermoregulation and the energetic significance of clustering behavior in the White-Backed Mousebird (*Colius colius*). *Physiological and Biochemical Zoology* **74**: 238-249.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2003. Facultative hypothermic responses in an Afrotropical arid-zone passerine, the red-headed finch (*Amadina erythrocephala*). *Journal of Comparative Physiology B* **173**: 339-346.

MCKECHNIE, A. E. & WOLF, B. O. 2004a. Partitioning of evaporative water loss in white-winged doves: plasticity in response to short-term thermal acclimation. *Journal of Experimental Biology* **207**: 203-210.

MCKECHNIE, A. E. & WOLF, B. O. 2004b. The allometry of avian basal metabolic rate: good predictions need good data. *Physiological and Biochemical Zoology* **77**: 502-521.

MCNAB, B. K. 1986. The influence of food habits on the energetics of eutherian mammals. *Ecological Monographs* **56**: 1-19.

MCNAB, B. K. 1988. Food habits and the basal rate of metabolism in birds. *Oecologia* **77**: 343-349.

MCNAB, B. K. 1997. On the utility of uniformity in the definition of basal rates of metabolism. *Physiological Zoology* **70**: 718-720.

MCNAB, B. K. 2001. Energetics of toucans, barbets and a hornbill: implications for avian frugivory. *Auk* **118**: 916-933.

MEROLA-ZWARTJES, M. & LIGON, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* **81**: 990-1002.

MIYAKI, C. Y., MATIOLI, S. R., BURKE, T., & WAJNTAL, A. 1998. Parrot evolution and paleogeographical events: mitochondrial DNA evidence. *Molecular Biology and Evolution* **15**: 544-551.

MOREAU, R. E. 1948. Aspects of the evolution in the parrot genus *Agapornis*. *Ibis* **90**: 206-239.

MUELLER, P. & DIAMOND, J. 2001. Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. *Proceedings of the National Academy of Sciences* **98**: 12550-12554.

PIERSMA, T., CADÉE, N., & DAAN, S. 1995. Seasonality in basal metabolic rate and thermal conductance in a long distance migrant shorebird, the knot (*Calidris canutus*). *Journal of Comparative Physiology* **165**: 37-45.

PIERSMA, T. & DRENT, J. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution* **18**: 228-233.

RACHELI, L. 1999. A cladistic analysis of the African parrot genus *Agapornis*. *Papageienkunde* **3**: 9-19.

REYNOLDS, P. S. & LEE, R. M. 1996. Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. *American Naturalist* **147**: 735-759.

SCHLEUCHER, E. 2002. Metabolism, body temperature and thermal conductance of fruit-doves (Aves: Columbidae, Treronidae). *Comparative Biochemistry and Physiology A* **131**: 417-428.

SCHLEUCHER, E. & WITHERS, P. C. 2002. Metabolic and thermal physiology of pigeons and doves. *Physiological and Biochemical Zoology* **75**: 439-450.

SIBLEY, C. G. & AHLQUIST, J. E. 1990. *Phylogeny and classification of birds.* Yale University Press, New Haven.

TIELEMAN, B. I. & WILLIAMS, J. B. 2000a. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**: 461-479.

TIELEMAN, B. I. & WILLIAMS, J. B. 2000b. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**: 461-479.

TIELEMAN, B. I., WILLIAMS, J. B., & BUSCHUR, M. E. 2002. Physiological adjustments to arid and mesic environments in Larks (*Alaudidae*). *Physiological and Biochemical Zoology* **75**: 305-313.

TIELEMAN, B. I., WILLIAMS, J. B., BUSCHUR, M. E., & BROWN, C. R. 2003. Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* **84**: 1800-1815.

WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia* **42**: 81-89.

WEATHERS, W. W., WEATHERS, D. L., & VAN RIPER, C. 1983. Basal metabolism of the Apapane: comparison of freshly caught birds with long-term captives. *The Auk* **100**: 977-978.

WHITE, C. R. & SEYMOUR, R. S. 2003. Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. *Proceedings of the National Academy of Sciences* **100**: 4046-4049.

WIKELSKI, M., SPINNEY, L., SCHELSKY, W., SCHEUERLEIN, A., & GWINNER, E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B* **270**: 2383-2388.

WILLIAMS, J. B., WITHERS, P. C., BRADSHAW, S. D., & NAGY, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Australian Journal of Zoology* **39**: 131-142.

CHAPTER FOUR

CONCLUSIONS

SUMMARY

The BMRs of lovebird and grass parakeet species were not correlated with deserticolous and non-deserticolous habitats representing an aridity gradient. The use of the phylogenetically independent contrasts (PIC) (Felsenstein 1985), to control for relatedness, paralleled the conventional ANOVA results, in not showing any significant differences between the physiological traits of deserticolous and non-deserticolous species.

The lack of significant differences in BMR between habitats supports the findings of Williams et al. (1991) who found no significant differences in the BMRs and field metabolic rates between deserticolous and non-deserticolous Australian parrots. The lack of a clear distinction in BMR between deserticolous and non-deserticolous parrots has several explanations. Phenotypic plasticity in the BMR of bird species may be expressed as lower BMRs when birds are acclimated to mesic conditions with a neutral photoperiod regime (12L:12D), such as those used in this study (Gabriel et al. 2005). Also, there is recent evidence that the scaling exponent of BMR differs between captive-raised and wild-caught birds (McKechnie et al. 2006), with all individuals used in this study being captive-raised. Deserticolous birds also often exhibit behavioural adaptations to the extreme environment in which they live (Wolf 2000). The use of thermal refugia during extremes of ambient temperature (T_a) has been shown to reduce energy expenditure and water loss (Williams et al. 1999). However, the behavioural responses of the study species to extreme T_as is unknown at this time. Another possible explanation is that birds in general are "pre-adapted" to deal with the extremes of desert environments (Maclean 1996). However, this standpoint does not explain the significant differences between desert and non-desert BMRs, for birds other than parrots, found by Tieleman and Williams (2000). The superimposition of the tenets of the "post arrival adaptation hypothesis" (Tieleman &

Williams 2000) on the concept of the "pre-adapted hypothesis" (Maclean 1996) helps to explain why some bird species in deserts show more extreme metabolic adaptations than other species. Some species exhibit adaptations beyond the "pre-adapted zone" characteristics of most birds.

Following the example of McKechnie et al. (2006), a large scale analysis of bird BMR data from the literature was undertaken, to determine the effect of origin (captive-raised vs. wild-caught). Whereas conventional analysis confirmed the finding of McKechnie et al. (2006), phylogenetically independent analysis found non-significant differences between captive-raised and wild-caught birds. Furthermore, the relationship between parrots and other birds was investigated, with conventional analysis showing significant differences in BMR between these two groups. Again the phylogenetically independent analysis disagreed with the conventional analysis findings, showing non-significant differences between parrots and other birds. The BMRs of captive-raised and wild-caught parrots were not significantly different using both conventional and phylogenetically independent analyses.

The findings of these large scale analyses seem to point to the fact that parrots do not conform to the patterns found for other birds. The BMRs of parrots appear to be unaffected by their origin, thus conclusions drawn regarding these BMRs may indeed be valid, irrespective of whether they were wild-caught or captive-raised.

It would be of interest to expand this analysis to include more parrot species, over a wider range of body mass, and to include a wider range of habitat types. The use of higher acclimation temperatures and longer photoperiods may be warranted in future studies of deserticolous birds in order to reduce the possibility of phenotypic plasticity masking the true BMRs of these species. No attempt was made to control for photoperiod in the large scale analyses, and this could have led to the masking of phenotypic signals. Many of the data used did not specify acclimation regimes and hence there is no standard measure available. The future measurement of reaction norms (high temperatures with long photoperiods and low temperatures with short photoperiods), as opposed to arbitrary acclimation regimes, is warranted since seasonal phenotypic plasticity is known in mammals and needs to be assessed in birds (Lovegrove 2005).

LITERATURE CITED

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125**: 1-15.

GABRIEL, W., LUTTBEG, B., SIH, A., & TOLLRIAN, R. 2005. Environmental tolerance, heterogeneity, and the evolution of reversible plastic responses. *American Naturalist* **166**: 339-353.

LOVEGROVE, B. G. 2005. Seasonal thermoregulatory responses in mammals. *Journal of Comparative Physiology B* **175**: 231-247.

MACLEAN, G. L. 1996. *Ecophysiology of Desert Birds*. Springer-Verlag, Berlin Heidelberg.

MCKECHNIE, A. E., FRECKLETON, R. P., & JETZ, W. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society of London B* **273**: 931-937.

TIELEMAN, B. I. & WILLIAMS, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**: 461-479.

WILLIAMS, J. B., TIELEMAN, B. I., & SHOBRAK, M. 1999. Lizard burrows provide thermal refugia for larks in the Arabian desert. *Condor* **101**: 714-717.

WILLIAMS, J. B., WITHERS, P. C., BRADSHAW, S. D., & NAGY, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Australian Journal of Zoology* **39**: 131-142.

WOLF, B. O. 2000. Global warming and avian occupancy of hot deserts: a physiological and behavioral perspective. *Revista Chilena de Historia Natural* **75**: 387-392.

APPENDIX ONE

Basal metabolic rate and body mass data for 242 bird species used in the analyses.

Species	Body mass (g)	BMR (W)	Origin	Reference
Apteryx owenii	1096	2.068	Captive-raised	Calder & Dawson 1978
Apteryx australis	2380	4.029	Captive-raised	Calder & Dawson 1978
Apteryx haasti	2450	4.179	Captive-raised	Calder & Dawson 1978
Callipepla gambelii	126.1	0.755	Wild caught	Weathers 1981
Bonasa umbellus	644	2.383	Captive-raised	Rasmussen & Brander 1973
Lagopus lagopus	567	2.872	Captive-raised	Kendeigh et al 1977
Tetrao urogallus	4010	11.816	Captive-raised	Kendeigh et al 1977
Dendragapus obscurus	1131	4.957	Wild caught	Pekins et al. 1992
Gallus gallus	2710	6.005	Captive-raised	Winchester 1940
Coturnix coturnix	89.5	0.820	Wild caught	Daan et al. 1990
Coturnix chinensis	44.9	0.368	Captive-raised	Roberts & Baudinette 1986
Coturnix pectoralis	95.8	0.635	Wild caught	Roberts & Baudinette 1986
Alectoris graeca	633	2.533	Captive-raised	Kendeigh et al 1977
Aythya fuligula	611	2.930	Wild caught	Daan et al. 1990
Branta bernicla	1253	6.060	Wild caught	Daan et al. 1990
Aix sponsa	448	2.247	Captive-raised	Kendeigh et al 1977
Anas penelope	723	2.799	Captive-raised	Kendeigh et al 1977

Anas platyrhynchos	741	3.400	Wild caught	Daan et al. 1990
Melanerpes formicivorus	73	0.737	Wild-caught	Weathers et al. 1990
Picoides pubescens	21.7	0.383	Wild-caught	Liknes & Swanson 1996
Picoides major	117	1.041	Captive-raised	Kendeigh et al 1977
Phoeniculus purpureus	74.07	0.174	Wild-caught	Boix-Hinzen & Lovegrove 1998
Trogon rufus	53	0.431	Wild caught	Yarbrough 1971
Alcedo atthis	34.3	0.378	Captive-raised	Kendeigh et al 1977
Merops viridis	33.8	0.295	Wild caught	Bryant et al. 1984
Colius striatus	51	0.236	Wild-caught	McKechnie & Lovegrove 2001
Colius colius	35.1	0.177	Wild-caught	McKechnie & Lovegrove 2001
Geococcyx californianus	284.7	1.462	Captive-raised	Calder & Schmidt-Nielsen 1967
Cacomantis variolosus	23.8	0.121	Wild caught	Hails 1983
Cuculus canorus	111.6	0.838	Captive-raised	Kendeigh et al 1977
Calyptorhynchus baudinii	597	2.698	Captive-raised	Cooper et al 2002
Calyptorhynchus latirostris	665	3.190	Captive-raised	Cooper et al 2002
Cacatua galerita	776.1	3.419	Wild caught	Williams et al. 1991
Cacactua tenuirostris	549.9	3.168	Wild caught	Williams et al. 1991
Eolophus roseicapillus	268.7	1.248	Wild caught	Williams et al. 1991
Agapornis canus	26.62	0.561	Captive-raised	Unpublished data from Perrin
Agapornis roseicollis	53.53	0.547	Captive-raised	This study
Agapornis nigrigenis	41.37	0.513	Captive-raised	This study
Agapornis fischeri	49.59	0.557	Captive-raised	This study
Agapornis personatus	46.77	0.506	Captive-raised	This study
Poicephalus meyeri	116.49	1.124	Captive-raised	Unpublished data from Perrin
Poicephalus rueppellii	106.94	0.907	Captive-raised	Unpublished data from Perrin
Poicephalus cryptoxanthus	138.22	1.126	Captive-raised	Unpublished data from Perrin
Melopsittacus undulatus	25.2	0.298	Captive-raised	Kendeigh et al 1977

Barnardius zonarius	137	0.718	Wild caught	Williams et al. 1991
Neopsephotus bourkii	42.75	0.487	Captive-raised	This study
Neophema petrophila	48.4	0.634	Wild caught	Williams et al. 1991
Neophema elegans	42.06	0.618	Captive-raised	This study
Neophema splendida	40.86	0.515	Captive-raised	This study
Neophema pulchella	41.90	0.578	Captive-raised	This study
Apus apus	44.9	0.436	Captive-raised	Kendeigh et al 1977
Collocalia esculenta	6.8	0.082	Wild caught	McNab & Bonaccorso 1995
Collocalia vanikorensis	11.6	0.120	Wild caught	McNab & Bonaccorso 1995
Oreotrochilus estella	8.1	0.192	Wild caught	Carpenter 1976
Sephanoides sephaniodes	5.74	0.102	Wild caught	Lopez-Calleja & Bozinovic 1995
Strix occidentalis	571	2.675	Wild caught	Ganey et al 1993
Nyctea scandiaca	2026	4.213	Wild caught	Gessaman 1972
Asio otus	252	0.954	Wild-caught	Wijnands 1984
Otus asio	166	0.586	Wild caught	Ligon 1969
Otus trichopsis	120	0.446	Captive-raised	Ligon 1969
Aegolius acadicus	124	0.654	Wild caught	Ligon 1969
Glaucidium gnoma	54	0.441	Wild caught	Ligon 1969
Podargus strigoides	380.3	1.033	Wild-caught	McNab & B 1995; Bech and Nicol, 1999
Podargus ocellatus	145	0.567	Wild caught	Lasiewski et al. 1970
Podargus papuensis	314.6	1.071	Wild caught	McNab & Bonaccorso 1995
Eurostopodus argus	88	0.407	Wild caught	Dawson & Fisher 1969
Chordeiles minor	72	0.441	Wild-caught	Lasiewski & Dawson 1964
Columba leucomela	456	2.437	Captive-raised	Schleucher and Withers 2002
Ocyphaps lophotes	187	1.085	Captive-raised	Schleucher and Withers 2002
Geophaps plumifera	81	0.394	Wild caught	Withers & Williams 1990
Geophaps smithii	198	0.873	Captive-raised	Schleucher and Withers 2002

Phaps elegans	190	1.238	Captive-raised	Schleucher and Withers 2002
Phaps chalcoptera	304	1.529	Captive-raised	Schleucher and Withers 2002
Phaps histrionica	257	1.297	Captive-raised	Schleucher and Withers 2002
Leucosarcia melanoleuca	445	1.695	Captive-raised	Schleucher and Withers 2002
Geopelia cuneata	39	0.266	Captive-raised	Schleucher and Withers 2002
Geopelia placida	52	0.355	Captive-raised	Schleucher and Withers 2002
Chalcophaps indica	124	0.793	Captive-raised	Schleucher and Withers 2002
Leptotila verreauxi	131	0.886	Wild caught	Vleck & Vleck 1979
Streptopelia senegalensis	108	0.847	Captive-raised	Kendeigh et al 1977
Streptopelia turtur	154	1.138	Captive-raised	Kendeigh et al 1977
Streptopelia decaocto	170	0.950	Wild caught	Daan et al. 1990
Scardafella inca	40.5	0.252	Wild-caught	MacMillen & Trost 1965
Ptilinopus melanospila	98	0.488	Captive-raised	Schleucher 2002
Ptilinopus superbus	120.4	0.756	Captive-raised	Schleucher 1999
Fulica atra	474	2.430	Wild caught	Daan et al. 1990
Pterocles orientalis	386.4	1.947	Wild-caught	Hinsley et al. 1993
Scolopax rusticola	430	2.160	Captive-raised	Kendeigh et al 1977
Scolopax minor	156.7	1.066	Captive-raised	Vander Haegen et al 1994
Limosa lapponica	240	1.520	Wild caught	Daan et al. 1990
Arenaria interpres	90	0.920	Wild caught	Kersten & Piersma 1987
Calidris canutus	130	0.880	Wild caught	Piersma et al 1995
Charadrius dubius	36	0.416	Captive-raised	Kendeigh et al 1977
Pluvialis squatarola	226	1.780	Wild caught	Kersten & Piersma 1987
Pluvialis apricarius	159	1.240	Wild caught	Daan et al. 1990
Haematopus ostralegus	449	2.910	Wild caught	Daan et al. 1990
Daptrius ater	362	1.199	Captive-raised	Wasser 1986
Falco tinnunculus	203	0.970	Wild caught	Daan et al. 1990

Falco subbuteo	208	1.298	Captive-raised	Kendeigh et al 1977
Falco mexicanus	430	1.943	Captive-raised	Wasser 1986
Accipiter cooperii	452	2.128	Captive-raised	Wasser 1986
Accipiter nisus	135	0.949	Captive-raised	Kendeigh et al 1977
Accipiter striatus	83	0.700	Captive-raised	Wasser 1986
Buteo lineatus	658	2.110	Captive-raised	Wasser 1986
Parabuteo unicinctus	572	1.407	Captive-raised	Wasser 1986
Aquila rapax	2398	4.520	Captive-raised	Wasser 1986
Pernis apivorus	652	2.319	Captive-raised	Kendeigh et al 1977
Anhinga rufa (anhinga)	1040	3.191	Captive-raised	Henneman 1983
Phalacrocorax auritus	1330	5.492	Captive-raised	Henneman 1983
Xiphorhynchus guttatus	45.2	0.446	Wild caught	Vleck & Vleck 1979
Thamnophilus punctatus	21	0.344	Wild caught	Vleck & Vleck 1979
Phytotoma rara	42	0.499	Wild-caught	Rezende et al 2001
Pipra mentalis	12.3	0.194	Wild caught	Bartholomew et al 1983
Manacus vitellinus	15.5	0.232	Wild caught	Bartholomew et al 1983
Sayornis phoebe	21.6	0.344	Wild caught	Yarbrough 1971
Contopus virens	13.9	0.257	Wild caught	Yarbrough 1971
Empidonax virescens	12.3	0.179	Wild caught	Yarbrough 1971
Tyrannus tyrannus	35.7	0.436	Wild caught	Yarbrough 1971
Myiarchus crinitus	33.9	0.383	Wild caught	Yarbrough 1971
Acanthorhynchus tenuirostris	9.7	0.249	Wild caught	Weathers et al 1996
Melithreptus lunatus	14.3	0.249	Wild caught	Vitali et al. 1999
Lichenostomus virescens	25	0.354	Wild caught	Collins et al. 1980
Lichmera indistincta	9	0.208	Wild caught	Collins et al. 1980
Phylidonyris novaehollandiae	17.3	0.317	Wild caught	Weathers et al 1996
Phylidonyris melanops	18.8	0.293	Wild caught	Vitali et al. 1999

Chloropsis sonnerati	39.7	0.378	Wild caught	Hails 1983
Lanius excubitor	72.4	0.814	Captive-raised	Kendeigh et al 1977
Lanius collurio	27	0.383	Captive-raised	Kendeigh et al 1977
Cyanocitta cristata	80.8	0.826	Wild caught	Misch 1960
Nucifraga caryocatactes	147	1.346	Captive-raised	Kendeigh et al 1977
Corvus monedula	188	1.720	Wild caught	Daan et al. 1990
Corvus corone	516	2.950	Wild caught	Daan et al. 1990
Pica pica	158.9	1.196	Wild caught	Hayworth & Weathers 1984
Pica nuttalli	151.9	1.467	Wild caught	Hayworth & Weathers 1984
Oriolus oriolus	64.9	0.649	Captive-raised	Kendeigh et al 1977
Bombycilla garrulus	72.5	0.954	Captive-raised	Kendeigh et al 1977
Sialia mexicana	27.5	0.423	Wild caught	Mock 1991
Turdus viscivorus	108.2	1.104	Captive-raised	Kendeigh et al 1977
Turdus iliacus	58	0.722	Captive-raised	Kendeigh et al 1977
Turdus philomelos	62.8	0.726	Captive-raised	Gavrilov 1974
Turdus merula	66.8	0.740	Wild caught	Daan et al. 1990
Ficedula hypoleuca	11.7	0.232	Captive-raised	Kendeigh et al 1977
Muscicapa striata	14.4	0.247	Captive-raised	Kendeigh et al 1977
Copsychus saularis	33.5	0.232	Wild caught	Hails 1983
Phoenicurus phoenicurus	13	0.232	Captive-raised	Kendeigh et al 1977
Erithacus rubecula	15.5	0.280	Wild caught	Daan et al. 1990
Acridotheres cristatellus	109.4	1.206	Wild caught	Johnson & Cowan 1975
Sturnus vulgaris	75	0.877	Captive-raised	Kendeigh et al 1977
Troglodytes aedon	10	0.190	Wild caught	Dutenhoffer & Swanson 1996
Troglodytes troglodytes	9	0.213	Captive-raised	Gavrilov 1974
Parus atricapillus	10.3	0.252	Wild caught	Rising & Hudson 1974
Parus major	16	0.300	Wild caught	Daan et al. 1990

Aegithalos caudatus	8.9	0.199	Captive-raised	Gavrilov 1974
Psaltriparus minimus	5.5	0.121	Wild-caught	Chaplin 1982
Hirundo tahitica	14.1	0.179	Wild caught	Bryant et al. 1984
Hirundo rustica	18	0.315	Captive-raised	Gavrilov 1974
Riparia riparia	13.6	0.232	Captive-raised	Kendeigh et al 1977
Regulus regulus	5.5	0.184	Captive-raised	Kendeigh et al 1977
Alophoixus bres	35	0.354	Wild caught	Hails 1983
Pycnonotus finlaysoni	26.3	0.221	Wild caught	Hails 1983
Pycnonotus goiavier	28.6	0.247	Wild caught	Hails 1983
Zosterops lateralis	11	0.149	Wild caught	Maddocks & Geiser 1997
Acrocephalus palustris	10.8	0.203	Captive-raised	Kendeigh et al 1977
Acrocephalus schoenobaenus	11.5	0.218	Captive-raised	Kendeigh et al 1977
Hippolais icterina	12.5	0.252	Captive-raised	Kendeigh et al 1977
Phylloscopus collybita	8.2	0.165	Captive-raised	Kendeigh et al 1977
Phylloscopus trochilus	10.7	0.208	Captive-raised	Kendeigh et al 1977
Malacopteron cinereum	15.8	0.213	Wild caught	Hails 1983
Sylvia borin	24.8	0.416	Captive-raised	Kendeigh et al 1977
Sylivia atricapilla	21.9	0.413	Captive-raised	Kendeigh et al 1977
Sylvia curruca	10.6	0.199	Captive-raised	Kendeigh et al 1977
Eremophila alpestris	26	0.310	Wild caught	Trost 1972
Alauda arvensis	31.7	0.722	Wild caught	Tieleman et al 2002
Lullula arborea	25.5	0.572	Wild caught	Tieleman et al 2002
Eremalauda dunni	20.6	0.278	Wild caught	Tieleman et al 2002
Certhilauda erythrochlamys	27.3	0.412	Wild caught	Williams 2000
Alaemon alaudipes	37.7	0.427	Wild caught	Tieleman et al 2002
Passer domesticus	24.2	0.280	Wild caught	Daan et al. 1990
Anthus pratensis	18.9	0.300	Captive-raised	Kendeigh et al 1977

Anthus trivialis	19.7	0.339	Captive-raised	Kendeigh et al 1977
Anthus campestris	21.8	0.383	Captive-raised	Kendeigh et al 1977
Motacilla alba	18	0.300	Captive-raised	Gavrilov 1974
Motacilla flava	14.7	0.257	Captive-raised	Kendeigh et al 1977
Prunella modularis	16.8	0.324	Captive-raised	Kendeigh et al 1977
Lonchura striata	12.1	0.200	Wild caught	Daan et al. 1990
Lonchura fuscans	9.5	0.097	Wild caught	Weathers 1977
Lonchura malacca	11.8	0.140	Wild caught	Hails 1983
Lonchura maja	12.8	0.150	Wild caught	Hails 1983
Spermetes cucullatus	10.62	0.078	Wild caught	Lovegrove & Smith (in press)
Poephila guttata	10.8	0.160	Wild caught	Daan et al. 1990
Padda oryzivora	25.4	0.308	Captive-raised	Marschall & Prinzinger 1991
Amadina fasciata	17.2	0.214	Captive-raised	Marschall & Prinzinger 1991
Amadina erythrocephala	22.4	0.213	Wild caught	McKechnie & Lovegrove in press
Estrilda melpoda	7.5	0.131	Captive-raised	Marschall & Prinzinger 1991
Arachnothera longirostra	13	0.189	Wild caught	Hails 1983
Aethopyga christinae	5.2	0.118	Wild caught	Prinzinger et al. 1989
Nectarinia venusta	7.1	0.140	Wild caught	Prinzinger et al. 1989
Fringilla coelebs	21	0.373	Captive-raised	Gavrilov 1974
Fringilla montifringilla	21	0.383	Captive-raised	Kendeigh et al 1977
Coccothraustes coccothraustes	48.3	0.691	Captive-raised	Kendeigh et al 1977
Loxia pytyopsittacus	53.7	0.792	Captive-raised	Kendeigh et al 1977
Carduelis chloris	28.2	0.470	Captive-raised	Kendeigh et al 1977
Carduelis pinus	14	0.291	Captive-raised	Gavrilov 1974
Carduelis tristis	13.6	0.334	Wild caught	Dawson & Carey 1976
Carpodacus erythrinus	21.6	0.358	Captive-raised	Gavrilov 1974
Carpodacus mexicanus	20.4	0.310	Wild caught	Weathers 1981

Carpodacus cassinii	27.4	0.339	Wild caught	Weathers 1981
Himatione sanguinea	13.5	0.300	Wild caught	Weathers et al 1983
Loxoides baileui	36	0.463	Wild caught	Weathers & Van Riper 1982
Amphispiza bilineata	11.6	0.197	Wild caught	Weathers 1981
Melospiza melodia	19.1	0.250	Wild caught	Yarbrough 1971
Melospiza georgiana	14.9	0.211	Wild caught	Yarbrough 1971
Zonotrichia querula	33.3	0.446	Wild caught	Yarbrough 1971
Zonotrichia leucophrys	26.1	0.336	Wild caught	Yarbrough 1971
Zonotrichia albicollis	20.2	0.278	Wild caught	Yarbrough 1971
Spizella arborea	19	0.439	Wild caught	Dutenhoffer & Swanson 1996
Spizella passerina	11.9	0.194	Wild caught	Yarbrough 1971
Spizella pusilla	13	0.264	Wild caught	Dutenhoffer & Swanson 1996
Junco hyemalis	18	0.295	Wild caught	Weathers & Sullivan 1993
Ammodramus savannarum	13.8	0.178	Wild caught	Yarbrough 1971
Passerculus sandwichensis	15.9	0.221	Wild caught	Williams & Hansell 1981
Pooecetes gramineus	21.5	0.271	Wild caught	Yarbrough 1971
Emberiza citrinella	26.8	0.436	Captive-raised	Gavrilov 1974
Emberiza hortulana	27	0.407	Captive-raised	Gavrilov 1974
Emberiza schoeniclus	17.6	0.300	Captive-raised	Kendeigh et al 1977
Seiurus aurocapillus	19	0.240	Wild caught	Yarbrough 1971
Protonotaria citrea	12.8	0.199	Wild caught	Yarbrough 1971
Geothlypis trichas	10.6	0.173	Wild caught	Yarbrough 1971
Mniotilta varia	8.2	0.125	Wild caught	Yarbrough 1971
Wilsonia citrina	12	0.211	Wild caught	Yarbrough 1971
Vermivora pinus	7.8	0.150	Wild caught	Yarbrough 1971
Seiurus noveboracensis	18.7	0.278	Wild caught	Yarbrough 1971
Dendroica dominica	9.8	0.160	Wild caught	Yarbrough 1971

Dendroica palmarum	9.8	0.155	Wild caught	Yarbrough 1971
Dendroica coronata	11.5	0.189	Wild caught	Yarbrough 1971
Dendroica pinus	12	0.179	Wild caught	Yarbrough 1971
Icterus galbula	37.5	0.504	Wild caught	Rising 1969
Cardinalis cardinalis	41	0.504	Wild caught	Hinds & Calder 1973
Cardinalis sinuata	32	0.392	Wild caught	Hinds & Calder 1973
Saltator coerulescens	47	0.389	Wild caught	Bosque at al 1999
Saltator orenocensis	32.7	0.314	Wild caught	Bosque at al 1999
Coereba flaveola	10	0.215	Wild caught	Merola-Zwartjes 1998

LITERATURE CITED

BARTHOLOMEW, G. A., VLECK, C. M., & BUCHER, T. L. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis* . *Physiological Zoology* **56**: 370-379.

BECH, C. & NICOL, S. C. 1999. Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. *Australian Journal of Zoology* **47**: 143-153.

BOIX-HINZEN, C. & LOVEGROVE, B. G. 1998. Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *Journal of Zoology, London* **244**: 33-41.

BOSQUE, C., PACHECO, M. A., & SIEGEL, R. B. 1999. Maintenance energy costs of two partially folivorous tropical passerines. *Auk* **116**: 246-252.

BRYANT, D. M., HAILS, C. J., & TATNER, P. 1984. Reproductive energetics of two tropical bird species. *Auk* **101**: 25-37.

CALDER, W. A. & DAWSON, T. J. 1978. Resting metabolic rates of ratite birds: the kiwis and the emu. *Comparative Biochemistry and Physiology* **60A**: 479-481.

CALDER, W. A. & SCHMIDT-NIELSEN, K. 1967. Temperature regulation and evaporation in the pigeon and the roadrunner. *American Journal of Physiology* **213**: 883-889.

CARPENTER, F. L. 1976. *Ecology and evolution of an Andean hummingbird (Oreotrochilus estella).* University of California Press, Berkeley.

CHAPLIN, S. B. 1982. The energetic significance of huddling in common bushtits (*Psaltriparus minimus*). *Auk* **99**: 424-430.

COLLINS, B. G., CARY, G., & PAYNE, S. 1980. Metabolism, thermoregulation and evaporative water loss in two species of Australian nectar-feeding birds (family Meliphagidae). *Comparative Biochemistry and Physiology* **67A**: 629-635.

COOPER, C. E., WITHERS, P. C., MAWSON, P. R., BRADSHAW, S. D., PRINCE, J., & ROBERSTON, H. 2002. Metabolic ecology of cockatoos in the south-west of western Australia. *Australian Journal of Zoology* **50**: 67-76.

DAAN, S., MASMAN, D., & GROENEWOLD, A. 1990. Avian basal metabolic rates: their association with body compostition and energy expenditure in nature. *American Journal of Physiology* **259**: R333 - R340-

DAWSON, W. R. & CAREY, C. 1976. Seasonal acclimation to temperature in Cardueline finches. *Journal of Comparative Physiology* **112**: 317-333.

DUTENHOFFER, M. S. & SWANSON, D. L. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution on endothermy. *Physiological Zoology* **69**: 1232-1254.

GANEY, J. L., BALDA, R. P., & KING, R. M. 1993. Metabolic rate and evaporative water loss of Mexican spotted and great horned owls. *Wilson Bulletin* **105**: 645-656.

GAVRILOV, V. M. 1974. Sezonnye i sutochnye izmeneniya urovnya standartnogo metabolizma u vorob'inykh ptits. In: *Materialy VI Vsesoyuznoï Ornitologicheskoï Konferentsii, Moskva - 1-5 fevralya 1974 goda.*, (eds.) R. L. Beme & V. E. Flint. Izdatel'stvo Moskovskogo Universiteta, Moskva.

GESSAMAN, J. A. 1972. Bioenergetics of the snowy owl (*Nyctea scandiaca*). *Arctic and Alpine Research* **4**: 223-238.

HAILS, C. J. 1983. The metabolic rate of tropical birds. *Condor* **85**: 61-65.

HAYWORTH, A. M. & WEATHERS, W. W. 1984. Temperature regulation and climatic adaptation in black-billed and yellow-billed magpies. *Condor* **86**: 19-26.

HENNEMANN, W. W. 1983. Environmental influences on the energetics and behavior of anhingas and double-crested cormorants. *Physiological Zoology* **56**: 201-216.

HINDS, D. S. & CALDER, W. A. 1973. Temperature regulation of the pyrrhuloxia and the Arizona cardinal.

HINSLEY, S. A., FERNS, P. N., THOMAS, D. H., & PINSHOW, B. 1993. Black-bellied sandgrouse (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiological Zoology* **66**: 20-42.

JOHNSON, S. R. & MCTAGGART COWAN, I. 1975. The energy cycle and thermal tolerance of starlings (Aves, Sturnidae) in North America. *Canadian Journal of Zoology* **53**: 55-68.

KENDEIGH, S. C., DOL'NIK, V. R., and GAVRILOV, V. M. 1977. Avian energetics. In: *Granivorous birds in ecosystems,* (eds.) J. Pinowski & S. C. Kendeigh. Cambridge University Press, Cambridge.

KERSTEN, M. & PIERSMA, T. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**: 175-187.

LASIEWSKI, R. C. & DAWSON, W. R. 1964. Physiological responses to temperature in the common nighthawk. *Condor* **66**: 477-490.

LASIEWSKI, R. C., DAWSON, W. R., & BARTHOLOMEW, G. A. 1970. Temperature regulation in the little Papuan frogmouth, *Podargus ocellatus*. *Condor* **72**: 332-338.

LIGON, J. D. 1969. Some aspects of temperature relations in small owls. *Auk* **86**: 458-472.

LIKNES, E. T. & SWANSON, D. L. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in white-breasted nuthatches *Sitta carolensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. *Journal of Avian Biology* **27**: 279-288.

LOPEZ-CALLEJA, M. V. & BOZINOVIC, F. 1995. Maximum metabolic rate, thermal insulation and aerobic scope in a small-sized Chilean hummingbird (*Sephanoides sephanoides*). *Auk* **112**: 1034-1036.

LOVEGROVE, B. G. & SMITH, G. A. 2003. Is "nocturnal hypothermia" a valid physiological concept in birds?: a study on Bronze Mannikins (*Spermetes cucullatus*). *Ibis* **145**: 547-557.

MACMILLEN, R. E. & TROST, C. H. 1967. Nocturnal hypothermia in the inca dove *Scardafella inca*. *Comparative Biochemistry and Physiology* **23**: 243-253.

MADDOCKS, T. A. & GEISER, F. 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* **99**: 104-112.

MARSCHALL, U. & PRINZINGER, R. 1991. Vergleichende Ökophysiologie von fünf Prachtfinkenarten (Estrilididae). *Journal für Ornithologie* **132**: 319-323.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2001a. Heterothermic responses in the speckled mousebird (*Colius striatus*). *Journal of Comparative Physiology B* **171**: 507-518.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2001b. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiological and Biochemical Zoology* **74**: 238-249.

MCKECHNIE, A. E. & LOVEGROVE, B. G. 2003. Facultative hypothermic responses in an Afrotropical arid-zone passerine, the red-headed finch (*Amadina erythrocephala*). *Journal of Comparative Physiology B* **173**: 339-346.

MCNAB, B. K. & BONACCORSO, F. J. 1995. The energetics of Australasian swifts, frogmouths and nightjars. *Physiological Zoology* **68**: 245-261.

MEROLA-ZWARTJES, M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost nests in the bananaquit (*Coereba flaveola*). *Auk* **115**: 780-786.

MISCH, M. S. 1960. Heat regulation in the northern blue jay, *Cyanocitta cristata bromia* Oberholser. *Physiological Zoology* **33**: 252-259.

MOCK, P. J. 1991. Daily allocation of time and energy of western bluebirds feeding nestlings. *Condor* **93**: 598-611.

PEKINS, P. J., GESSAMAN, J. A., & LINDZEY, F. G. 1992. Winter energy requirements of blue grouse. *Canadian Journal of Zoology* **70**: 22-24.

PIERSMA, T., CADÉE, N., & DAAN, S. 1995. Seasonality in basal metabolic rate and thermal conductance in a long distance migrant shorebird, the knot (*Calidris canutus*). *Journal of Comparative Physiology* **165**: 37-45.

PRINZINGER, R., LÜBBEN, I., & SCHUCHMANN, K. L. 1989. Energy metabolism and body temperature in 13 sunbird species (Nectariniidae). *Comparative Biochemistry and Physiology* **92A**: 393-402.

RASMUSSEN, G. & BRANDER, R. 1973. Standard metabolic rate and lower critical temperature for the ruffed grouse. *Wilson Bulletin* **85**: 223-229.

REZENDE, E. L., LOPEZ-CALLEJA, M. V., & BOZINOVIC, F. 2001. Standard and comparative energetics of a small avian herbivore (*Phytotoma rara*). *Auk* **118**: 781-785.

RISING, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology* **31**: 915-925.

RISING, J. D. & HUDSON, J. W. 1974. Seasonal variation in the metabolism and thyroid activity of the black-capped chickadee (*Parus atricapillus*). *Condor* **76**: 198-203.

ROBERTS, J. R. & BAUDINETTE, R. V. 1986. Thermoregulation, oxygen consumption and water turnover in stubble quail, *Coturnix pectoralis*, and king quail, *Coturnix chinensis*. *Australian Journal of Zoology* **34**: 25-33.

SCHLEUCHER, E. 1999. Energy metabolism in an obligate frugivore, the superb fruit-dove (*Ptilinopus superbus*). *Australian Journal of Zoology* **47**: 169-179.

SCHLEUCHER, E. 2002. Metabolism, body temperature and thermal conductance of fruit-doves (Aves: Columbidae, Treronidae). *Comparative Biochemistry and Physiology A* **131**: 417-428.

SCHLEUCHER, E. & WITHERS, P. C. 2002. Metabolic and thermal physiology of doves and pigeons. *Physiological and Biochemical Zoology* **75**: 439-450.

TIELEMAN, B. I., WILLIAMS, J. B., & BUSCHUR, M. E. 2002. Physiological adjustments to arid and mesic environments in larks (Alaudidae). *Physiological and Biochemical Zoology* **75**: 305-313.

TROST, C. H. 1972. Adaptations of horned larks (*Eremophila alpestris*) to hot environments. *Auk* **89**: 506-527.

VANDER HAEGEN, W. M., OWEN, R. B., & KROHN, W. B. 1994. Metabolic rate of American woodcock. *Wilson Bulletin* **106**: 338-343.

VITALI, S. D., WITHERS, P. C., & RICHARDSON, K. C. 1999. Standard metabolic rates of three nectarivorous meliphagid passerine birds. *Australian Journal of Zoology* **47**: 385-391.

VLECK, C. M. & VLECK, D. 1979. Metabolic rate in five tropical bird species. *Condor* **81**: 89-91.

WASSER, J. S. 1986. The relationship of energetics of falconiform birds to body mass and climate. *Condor* **88**: 57-62.

WEATHERS, W. W. 1977. Temperature regulation in the Dusky Munia, *Lonchura fuscans* (Cassin) (Estrildidae). *Australian Journal of Zoology* **25**: 193-199.

WEATHERS, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiological Zoology* **54**: 345-361.

WEATHERS, W. W., KOENIG, W. D., & STANBACK, M. T. 1990. Breeding energetics and thermal ecology of the acorn woodpecker in central coastal California. *Condor* **92**: 341-359.

WEATHERS, W. W., PATON, D. C., & SEYMOUR, R. S. 1996. Field metabolic rate and water flux of nectarivorous honeyeaters. *Australian Journal of Zoology* **44**: 445-460.

WEATHERS, W. W. & SULLIVAN, K. A. 1993. Seasonal patterns of time and energy allocation by birds. *Physiological Zoology* **66**: 511-536.

WEATHERS, W. W. & VAN RIPER, C. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palilia (*Psittirostra bailleui*) and the Laysan finch (*Psittirostra cantans*). *Auk* **99**: 667-674.

WEATHERS, W. W., WEATHERS, D. L., & VAN RIPER, C. 1983. Basal metabolism of the apapane: comparison of freshly caught birds with long-term captives. *Auk* **100**: 977-978.

WIJNANDTS, H. 1984. Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* **72**: 1-92.

WILLIAMS, J. B. 1999. Heat production and evaporative water loss of dune larks from the Namib desert. *Condor* **101**: 432-438.

WILLIAMS, J. B. & HANSELL, H. 1981. Bioenergetics of captive Belding's savannah sparrows (*Passerculus sandwichensis beldingi*). *Comparative Biochemistry and Physiology* **69A**: 783-787.

WILLIAMS, J. B., WITHERS, P. C., BRADSHAW, S. D., & NAGY, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Australian Journal of Zoology* **39**: 131-142.

WINCHESTER, C. F. 1940. *Seasonal and metabolic rhythms in the domestic fowl.* University of Missouri, Columbia, MO.

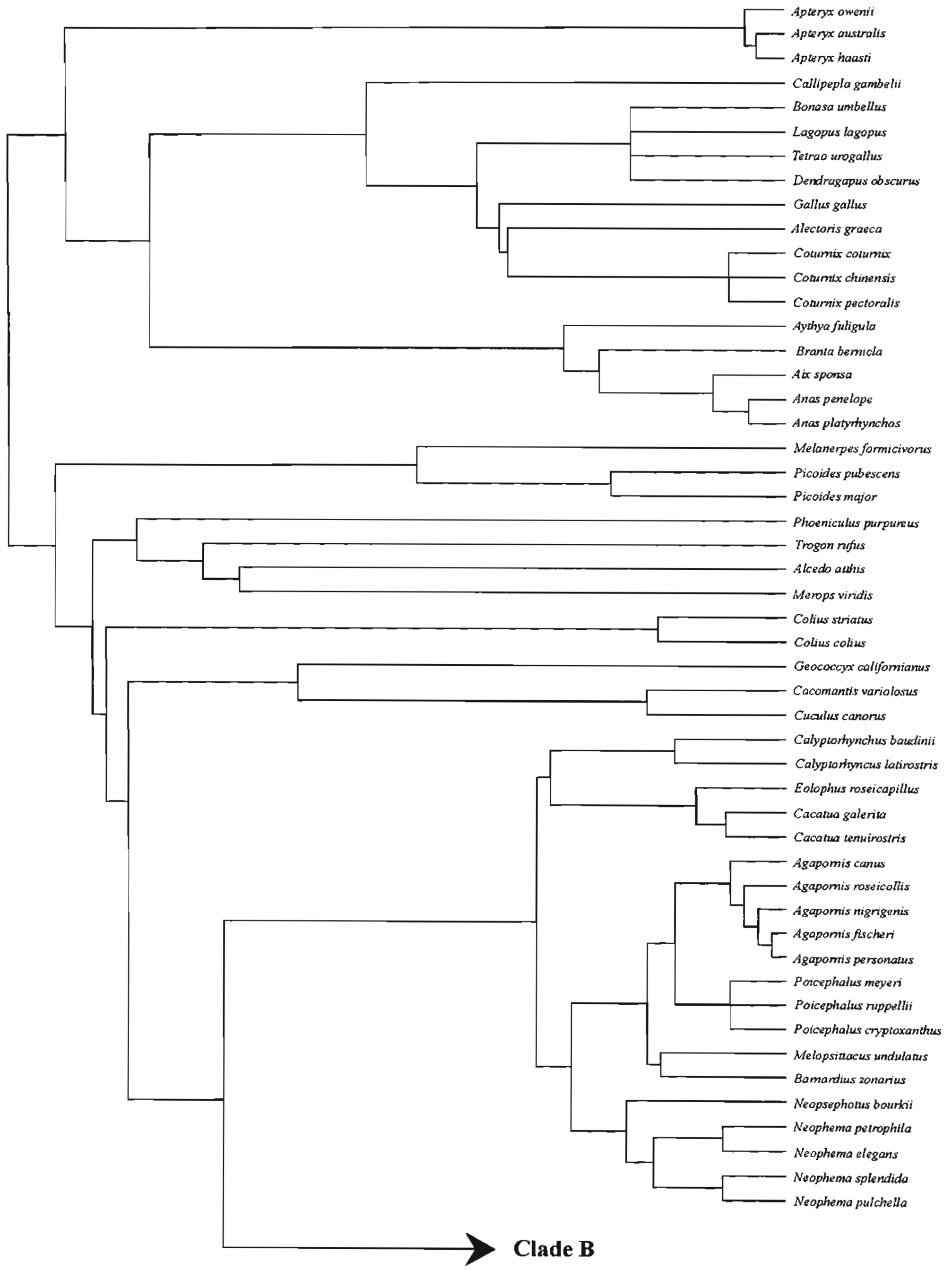
WITHERS, P. C. & WILLIAMS, J. B. 1990. Metabolic and respiratory physiology of an arid-adapted Australasian bird, the Spinifex pigeon. *Condor* **92**: 961-969.

YARBROUGH, C. G. 1971. The influence of distribution and ecology on the thermoregulation of small birds. *Comparative Biochemistry and Physiology* **39A**: 235-266.

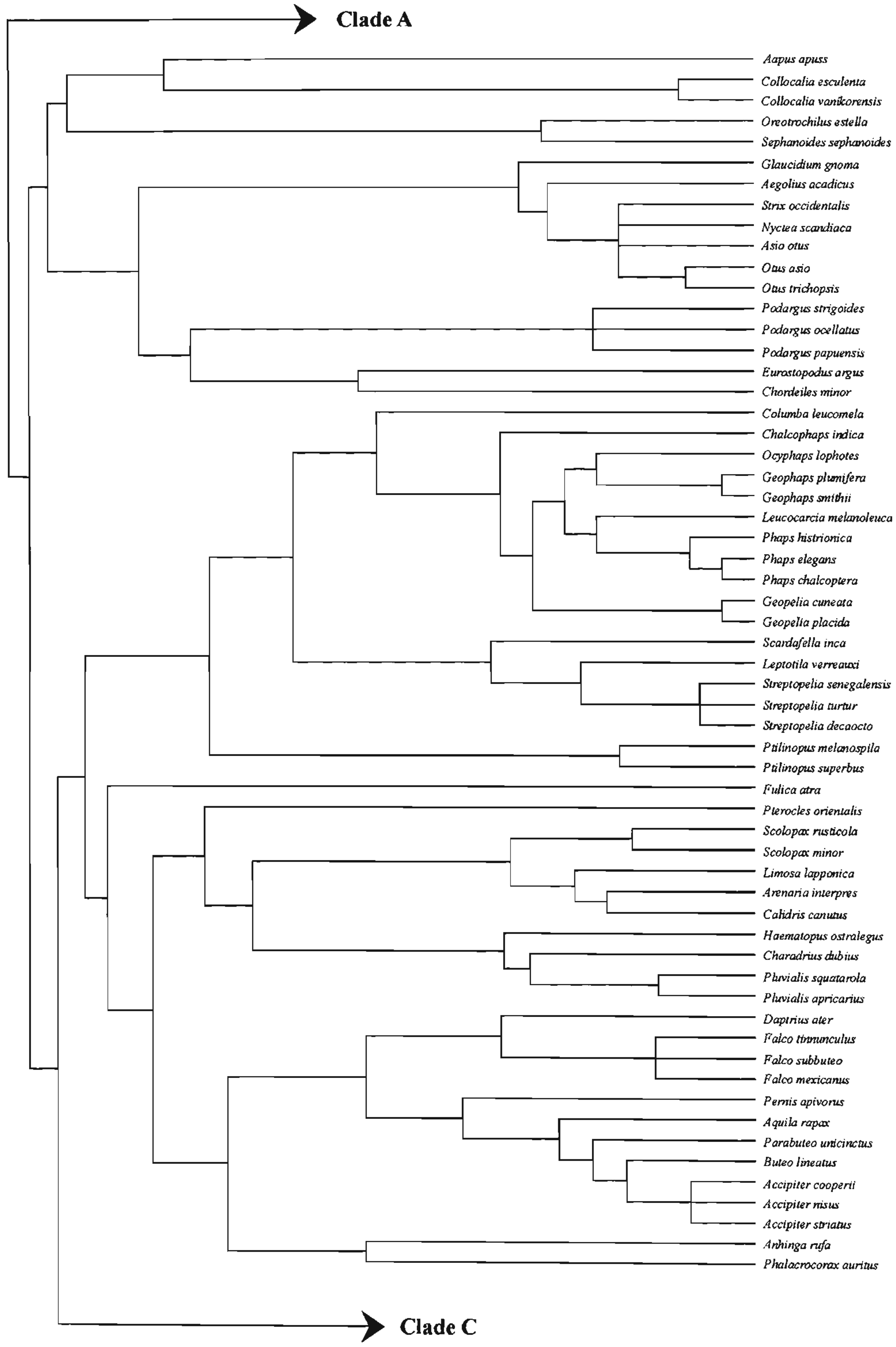
APPENDIX TWO

Phylogeny for 242 species used in analyses, constructed using morphological and molecular data from sources listed in text. For convenience, the phylogeny is split into four clades, namely A and B (non-passerines) and C and D (passerines).

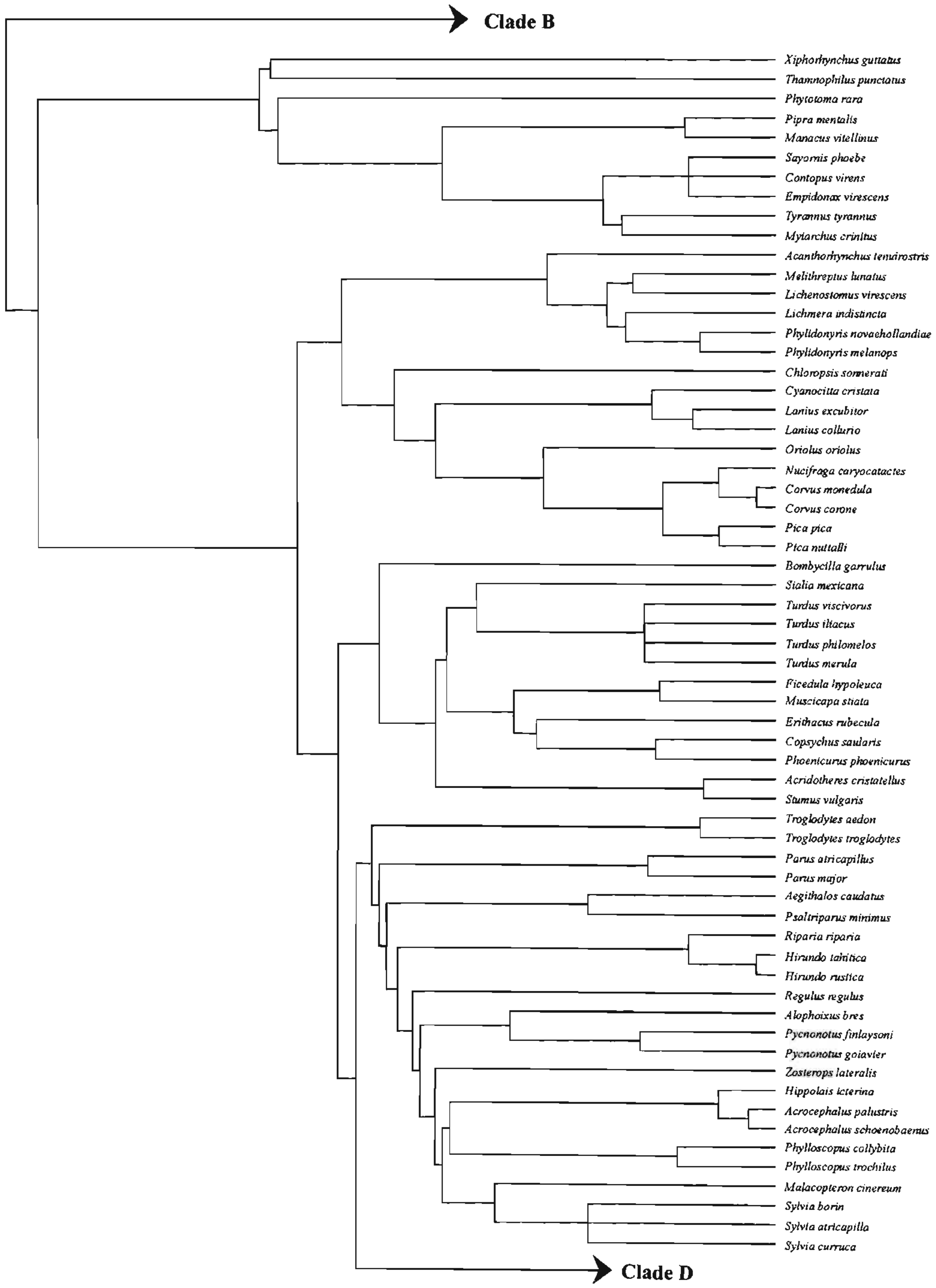
Clade A



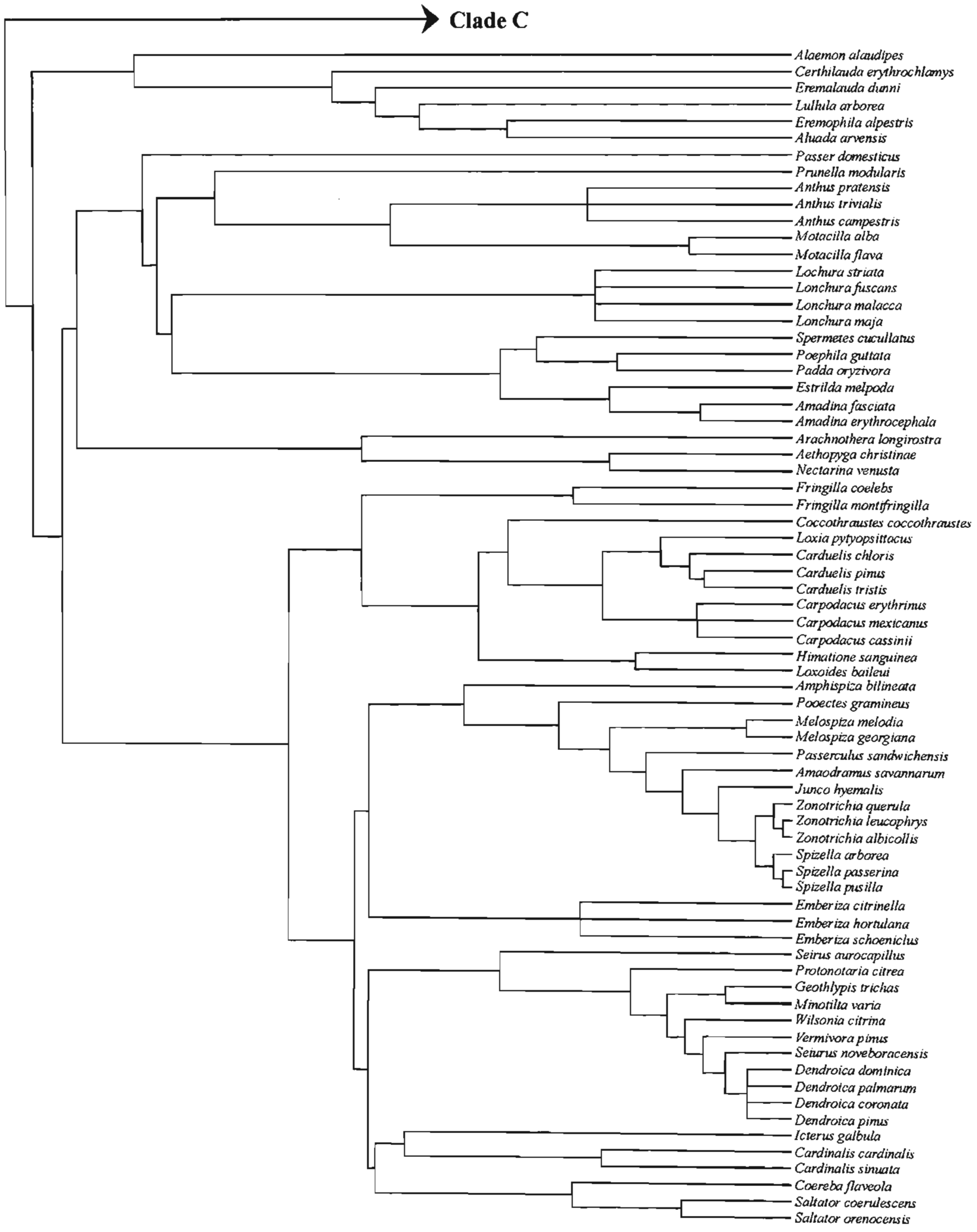
Clade B


Clade A
Aapus apuss
Collocalia esculenta
Collocalia vanikorensis
Oreotrochilus estella
Sephanoides sephanoides
Glaucidium gnoma
Aegolius acadicus
Strix occidentalis
Nyctea scandiaca
Asio otus
Otus asio
Otus trichopsis
Podargus strigoides
Podargus ocellatus
Podargus papuensis
Eurostopodus argus
Chordeiles minor
Columba leucomela
Chalcophaps indica
Ocyphaps lophotes
Geophaps plumifera
Geophaps smithii
Leucocarcia melanoleuca
Phaps histrionica
Phaps elegans
Phaps chalcoptera
Geopelia cuneata
Geopelia placida
Scardafella inca
Leptotila verreauxi
Streptopelia senegalensis
Streptopelia turtur
Streptopelia decaocto
Ptilinopus melanospila
Ptilinopus superbus
Fulica atra
Pterocles orientalis
Scolopax rusticola
Scolopax minor
Limosa lapponica
Arenaria interpres
Calidris canutus
Haematopus ostralegus
Charadrius dubius
Pluvialis squatarola
Pluvialis apricarius
Daptrius ater
Falco tinnunculus
Falco subbuteo
Falco mexicanus
Pernis apivorus
Aquila rapax
Parabuteo unicinctus
Buteo lineatus
Accipiter cooperii
Accipiter nisus
Accipiter striatus
Anhinga rufa
Phalacrocorax auritus
Clade C

Clade C


Clade B
Xiphorhynchus guttatus
Thamnophilus punctatus
Phytotoma rara
Pipra mentalis
Manacus vitellinus
Sayornis phoebe
Contopus virens
Empidonax virescens
Tyrannus tyrannus
Mytarchus crinitus
Acanthorhynchus tenuirostris
Melithreptus lunatus
Lichenostomus virescens
Lichmera indistincta
Phylidonyris novaehollandiae
Phylidonyris melanops
Chloropsis sonnerati
Cyanocitta cristata
Lanius excubitor
Lanius collurio
Oriolus oriolus
Nucifraga caryocatactes
Corvus monedula
Corvus corone
Pica pica
Pica nuttalli
Bombycilla garrulus
Sialia mexicana
Turdus viscivorus
Turdus iliacus
Turdus philomelos
Turdus merula
Ficedula hypoleuca
Muscicapa stiata
Erithacus rubecula
Copsychus saularis
Phoenicurus phoenicurus
Acridotheres cristatellus
Sturnus vulgaris
Troglodytes aedon
Troglodytes troglodytes
Parus atricapillus
Parus major
Aegithalos caudatus
Psaltriparus minimus
Riparia riparia
Hirundo tahitica
Hirundo rustica
Regulus regulus
Alophoixus bres
Pycnonotus finlaysoni
Pycnonotus goiavier
Zosterops lateralis
Hippolais icterina
Acrocephalus palustris
Acrocephalus schoenobaenus
Phylloscopus collybita
Phylloscopus trochilus
Malacopteron cinereum
Sylvia borin
Sylvia atricapilla
Sylvia curruca
Clade D

Clade D


Clade C
Alaemon alaudipes
Certhilauda erythrochlamys
Eremalauda dunni
Lulhila arborea
Eremophila alpestris
Aluada arvensis
Passer domesticus
Prunella modularis
Anthus pratensis
Anthus trivialis
Anthus campestris
Motacilla alba
Motacilla flava
Lochura striata
Lonchura fuscans
Lonchura malacca
Lonchura maja
Spermetes cucullatus
Poephila guttata
Padda oryzivora
Estrilda melpoda
Amadina fasciata
Amadina erythrocephala
Arachnothera longirostra
Aethopyga christinae
Nectarina venusta
Fringilla coelebs
Fringilla montifringilla
Coccothraustes coccothraustes
Loxia pytyopsittacus
Carduelis chloris
Carduelis pimus
Carduelis tristis
Carpodacus erythrinus
Carpodacus mexicanus
Carpodacus cassinii
Himatione sanguinea
Loxoides baileui
Amphispiza bilineata
Pooectes gramineus
Melospiza melodia
Melospiza georgiana
Passerculus sandwichensis
Amaodramus savannarum
Junco hyemalis
Zonotrichia querula
Zonotrichia leucophrys
Zonotrichia albicollis
Spizella arborea
Spizella passerina
Spizella pusilla
Emberiza citrinella
Emberiza hortulana
Emberiza schoeniclus
Seirus aurocapillus
Protonotaria citrea
Geothlypis trichas
Minotilta varia
Wilsonia citrina
Vermivora pimus
Seiurus noveboracensis
Dendroica dominica
Dendroica palmarum
Dendroica coronata
Dendroica pimus
Icterus galbula
Cardinalis cardinalis
Cardinalis sinuata
Coereba flaveola
Saltator coerulescens
Saltator orenocensis

APPENDIX THREE

Phylogeny for 20 parrot species used in analyses, constructed using morphological and molecular data from sources listed in the text.