

# CONDITION OF PHALANGER RELATIONS: A REVIEW

A. J. BRADLEY<sup>2</sup>, R. A. HOW<sup>1</sup>, and J. L. BARNETT<sup>3</sup>

"Possums and Gliders" is a collection of more than 57 scientific research and review papers that describe the life history, taxonomy, physiology, behaviour and conservation of Australia's unique forest dwelling marsupials: the possums, gliders and Koala. Over 70 authors provide insights into the lives of these fascinating marsupials. Aspects of the general biology and life history of many rare or little known species are described for the first time. These accounts are integrated with reviews, and reappraisals of past research to give a comprehensive and up to date reference work that should appeal to the specialist as well as the general reader with an interest in the biology and conservation of Australia's native fauna.

The value of this informative text is enhanced by inclusion of a key and field guide, that provides an introduction to the distinguishing features, habitat preference, and distribution of all Australian species of possums and gliders. A species index allows users of the field guide to rapidly locate more detailed information about the biology of each species in the main text.

"Possums and Gliders" is divided into eight sections, the first dealing with aspects of general biology: evolutionary relationships, life histories, reproduction, behaviour, disease and condition. The next six sections consider specific aspects of the biology of individual species in the six separate families of possums, gliders and Koala. The last section is devoted to problems of conservation and management, an area receiving increasing attention as forest clearance and development threaten some rare and little known species.

"Possums and Gliders" is the first major book to be published by the Australian Mammal Society. It arises from the proceedings of the "Possum and Glider Symposium" held in Armidale, NSW in November 1983 to celebrate the 25th anniversary of the Society. Organization of the symposium and subsequent compiling and editing of "Possums and Gliders" reflects the great interest and enthusiasm of Dr. Andrew Smith and Associate Professor Ian Hume of the University of New England, Armidale for furthering our understanding of these little known, but endearing native inhabitants of Australia's forest and shrublands.

described in both popular and scientific literature by the commonly judged as a *gestalt* (fat, thin, sick, well, compared with other members of the set. The study covers an interzone between health, in a clinical or performance (fertility, growth rate . . .). Changes in cross condition indices (e.g. length<sup>3</sup>/weight), perhaps, but individual performance may be markedly influenced without concurrent changes in such indices. More (e.g. blood constituents) can be conducted but are difficult to measure. Both approaches have been used on phalanger *Trichosurus vulpecula* and *T. caninus* (Marsupialia): used show correlations with ecological performance. In *T. vulpecula* the data are consistent with, while in *T. caninus* they are consistent with stress, influencing fertility. Experimental manipulation of natural field observations but none have been conducted.

Genetics, feeding, nutrition, endocrinology, parasitology and methodology relevant to the condition indices, particularly, where data allow, in phalangers.

Possums, Condition, Condition Index, Health, Nutrition, Haematology, Corticosteroids, Population Biology.

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aspects of condition that lie in the field and the clinical themselves to examine are primarily aspects of condition and dimensions of demographic

performance. The demographic characteristics of some of the phalangers have been compared elsewhere (How 1978, Hocking 1981, Kerle 1984).

To correlate condition and demography requires long-term population studies and these are generally lacking. There are two long-term studies on phalanger populations, namely those on *Trichosurus vulpecula* (Kerr) in the Orongoro Valley, New Zealand and the same species and its congener *T. caninus* (Ogilby) at Clouds Creek in New South Wales. We will of necessity draw heavily on these, although there are relevant studies on other possums.

## ASSESSMENT OF CONDITION

While there is no general agreement on methods to assess condition, the available criteria fall into two broad categories — morphological and physiological.

### Morphological criteria

Parameters in this category can give some indication of overt condition of an animal. Examination of external morphology may indicate either

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# POSSUMS AND GLIDERS



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# 5. INDICES OF CONDITION OF PHALANGER POPULATIONS: A REVIEW

W. F. HUMPHREYS<sup>1</sup>, A. J. BRADLEY<sup>2</sup>, R. A. HOW<sup>1</sup>, and J. L. BARNETT<sup>3</sup>

The well being of organisms is described in both popular and scientific literature by the non-specific term 'condition' which is commonly judged as a *gestalt* (fat, thin, sick, well, drab, lethargic, sleek, senescent . . .) compared with other members of the set. The study of condition in natural populations covers an interzone between health, in a clinical or physiological sense, and ecological performance (fertility, growth rate . . .). Changes in condition are commonly measured by gross condition indices (e.g. length<sup>3</sup>/weight), perhaps calibrated against weight of fat depots, but individual performance may be markedly influenced, for example, by parasites without concurrent changes in such indices. More detailed investigations of condition (e.g. blood constituents) can be conducted but are difficult to interpret due to both a lack of 'normal values' and to measured levels of parameters probably resulting from several causes. Both approaches have been used on phalanger populations, mainly on *Trichosurus vulpecula* and *T. caninus* (Marsupialia: Phalangeridae). The condition indices used show correlations with ecological performance in both the spatial and temporal dimensions. In *T. vulpecula* the data are consistent with food resource regulation of breeding, while in *T. caninus* they are consistent with stress, induced by behavioural feedback, influencing fertility. Experimental manipulation of natural populations is needed to test some of the field observations but none have been conducted.

A synopsis is given of aspects of genetics, feeding, nutrition, endocrinology and methodology relevant to the measurement and interpretation of condition indices, particularly, where data allow, in phalangers.

Key Words: Phalangers, Marsupialia, Possums, Condition, Condition Index, Health, Nutrition, Haematology, Corticosteroids, Stress, Genetics, Parasitology, Population Biology.

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## INTRODUCTION

THE physical well being of organisms is generally described, in both popular and scientific works, by the non-specific term 'condition'. Condition is most commonly measured as a *gestalt* (thin, fat, well, drab, sick, lethargic, sleek, senescent . . .) compared with other members of the set. We know from experience that organisms in poor condition perform badly and sometimes die, so condition is related to evolutionary fitness. While the proximate causes and effects of poor condition are the concern of clinicians (pathologists, physiologists, biochemists . . .), the ecologist is more concerned with the ultimate effect of condition on individual fitness as it relates to populations and communities; consequently the ecologist is equally as interested in sickness as in health.

In this review we wish to address aspects of condition in phalanger populations that lie in the interzone between the ecological and the clinical view of condition. We confine ourselves to examining indices of condition, and are primarily concerned with changes in indices of condition in both the spatial and temporal dimensions and in their correlations with demographic

performance. The demographic characteristics of some of the phalangers have been compared elsewhere (How 1978, Hocking 1981, Kerle 1984).

To correlate condition and demography requires long-term population studies and these are generally lacking. There are two long-term studies on phalanger populations, namely those on *Trichosurus vulpecula* (Kerr) in the Orongoro Valley, New Zealand and the same species and its congener *T. caninus* (Ogilby) at Clouds Creek in New South Wales. We will of necessity draw heavily on these, although there are relevant studies on other possums.

## ASSESSMENT OF CONDITION

While there is no general agreement on methods to assess condition, the available criteria fall into two broad categories — morphological and physiological.

### *Morphological criteria*

Parameters in this category can give some indication of overt condition of an animal. Examination of external morphology may indicate either

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clinical or sub-clinical states due to parasite burdens and disease, or social status as a consequence of rump wear and skin lesions. Body weight measurements, especially if continued through time, give some indication of recent nutritional history. At slaughter, pathological states can be observed grossly, such as ulcers or adrenal hyperplasia, or histologically, such as changes in the proportion of lymphoid elements in the spleen.

One associated attribute of good condition is adequate reserves of energy and so measures of fat depots are probably a useful positive correlate of condition as they indicate energy reserves (but see below). These measures are sometimes direct (fat depth measurements at slaughter) but more frequently are indirect using either equations relating fat reserves with body weight (Bamford 1970), with water space (Macfarlane, Howard and Good 1974; Nagy and Costa 1980) or with a score indicating fat depth (Graham 1982). The choice of a derived equation or index measure of condition is probably a function of size. For example it is unlikely that the condition scoring system for cattle could be applied to a small rodent or even an animal the size of a Brushtail Possum, as subcutaneous fat depots probably vary only a few mm while that in cattle destined for slaughter range between 4 and 17 mm.

For a number of reasons condition scores based on fat depots could be misleading, especially if used to compare different populations. a) Different genetic stocks can vary considerably in the location of their fat depots (Pond 1981). b) The allocation of production between growth and reproduction is responsive to changes in nutrition. c) Individual size is important because, due to the scaling of respiration with body size, a fat reserve of 10% of body weight will last an individual half the weight of another only 84% as long. d) Fat depots may be for purposes other than energy storage, such as for balance, social signals (Pond 1981) and for insulation.

### **Physiological criteria**

While requiring a greater technological input than morphological criteria, physiological criteria are capable of providing considerable information for the assessment of condition. Physiological measures fall in two main classes: a) blood constituents and b) specific function tests.

a) Blood constituents can indicate nutritional status, short and long term stress, infections/diseases and water balance, but which measures are used depends on the particular environment and the purpose of the study. For example water balance is a potentially crucial element of condition in environments where water is limiting. However, there would probably be general agreement that in ecological studies it would be useful to have a measure of nutritional status, the

degree of stress and perhaps some measure of their seasonality.

Differences associated with diet occur in haemoglobin concentration in mice (Francis and Strong 1938) and dogs (Weech, Wollstein and Goettsch 1937) and dietary restrictions may lead to changes in serum protein (Weech, Goettsch and Reeves, 1935; Zeldis *et al.* 1945), plasma lipid concentrations (Zeldis *et al.* 1945) and red cell volume (Haxhe 1967) in dogs and to changes in plasma carbohydrate and cholesterol concentration in horses (Fonnesbeck and Symons 1969).

Stress usually involves the pituitary-adrenal axis, and changes to this system are generally measured in two ways. Firstly, adrenal activity can be measured directly by measuring plasma corticosteroid concentrations. Secondly, it can be measured indirectly by examining the differential white cell count or the metabolites of glucogenesis such as liver glycogen, plasma glucose and protein concentrations. A consequence of elevated corticosteroids is immunosuppression and, therefore, an assessment of the immune response can provide useful information on both stress and disease. All these criteria have been used to define the stress related mortality in male *Antechinus stuartii* (Barnett 1973; Cheal, Lee and Barnett 1976; Bradley, McDonald and Lee 1980) and other mammals (Dickens, 1978; Dieterich and Feist 1980).

Several blood parameters are affected by season and therefore it may be possible to use them to indicate the animals response to, or perception of, the seasonality of different environments. Parameters in this category are haemoglobin concentration, haematocrit and red blood cell count. Haemoglobin concentration, for example, changes seasonally in mice (Maclean and Lee 1973) and voles (Newson 1962), being highest in winter. In the voles, the changes were not correlated with age, breeding condition, weather or parasite infection (Newson 1962). Other evidence suggests that haemoglobin responds to abiotic factors (Sealander 1960) such as temperature, as found in the house mouse (Maclean and Lee 1973).

b) Functional tests can be used to assess the ability of particular systems to respond. For example, immunological competence can be assessed with an antigen challenge (Bradley, McDonald and Lee 1980), while adrenocortical function can be assessed using a number of clinical tests (Harper 1973; and in James and Landon 1968). While these latter tests are commonly used in the laboratory, they are rarely used in wild animals (Miller and Bradshaw 1979; I. R. McDonald, pers. comm.). Another less time consuming test of adrenal function, more easily applied in the field, is to subject the animals to a standard stressor such as diethyl ether (Barnett 1977). A variety of clinical tests also exist to assess liver function; under these conditions liver

specific enzymes are usually measured although we are unaware of them being applied in field studies; under such conditions liver specific enzymes are usually measured.

### PROBLEMS ASSOCIATED WITH BLOOD SAMPLING IN THE FIELD

These problems are of two type, methodological and animal.

#### *Methodological problems*

These problems arise particularly due to the diurnal pattern of secretion or metabolism of some blood metabolites, their partitioning within the blood and tissue, and the interdependency of various physiological systems. They are exemplified in measuring cortisol as an indicator of adrenal function but probably apply in total or in part to other blood parameters.

Cortisol has been described as the major glucocorticoid in marsupials (Chester-Jones *et al.* 1964; Weiss and McDonald 1966; Oddie 1976), however in some mammals the pattern of glucocorticoid secretion may change under certain conditions. Fevold and Drummond (1976) have described such a change in snowshoe hares during a population decline in the spring, in which cortisol, a more potent glucocorticoid than corticosterone, became the major peripheral glucocorticoid. It is conceivable that qualitative changes in glucocorticoids may occur in wild populations under conditions of stress, and this would have important implications for steroid partitioning in the plasma. Evidence is emerging from studies on marsupials that similar changes may sometimes occur (A. J. Bradley, unpublished).

It is considered that the glucocorticoid hormone in blood plasma is partitioned in such a way that about 80% is bound to high affinity corticosteroid binding globulin (CBG), about 10% loosely bound to albumin and the remainder is unbound (free; Tait and Burstein 1964). Much evidence indicates that only the free fraction is biologically active (see review of Ballard 1979). An increase in total glucocorticoid may arise from either an increase in corticosteroid production rate and/or a decrease in corticosteroid clearance rate. The latter could arise following a reduction in hepatic and renal blood flow as suggested from experiments on cold stress in sheep (Panaretto 1974).

While the above describe changes in total glucocorticoid, it is important to consider also the concentration of the steroid binding proteins, namely CBG and albumin. Liver function is also relevant as this organ is involved in the production of high affinity steroid binding proteins, both CBG and sex hormone binding protein (SBP) which has implications for steroid

dynamics of both glucocorticoids and sex hormones. Marsupials have been shown to possess these binding proteins (Sernia, Bradley and McDonald 1979; Bradley 1982) and phalangers have both CBG and SBP, although the latter is absent in some families. Another major plasma protein of hepatic origin is albumin which binds with steroid hormones with low affinity, but, in view of its high concentration in the blood of normal mammals, it is a significant competitor for steroid hormone binding. Bradley, Lee and McDonald (1980) showed the importance of elevated concentrations of unbound corticosteroid hormone in the post mating mortality in males of the dasyurid *Antechinus stuartii*. In this case the CBG concentration was depressed by an elevation in androgen, however there appears to be no such reciprocal relationship among the phalangers.

A major function of the liver is to clear unbound steroid hormones from the blood on a single passage through the organ (Tait and Burnstein 1964). Thus significant hepatocellular damage may affect both the synthetic capacity of the liver and its function in clearance of steroid hormones. Among phalangers, production and clearance rates have only been measured in captive *T. vulpecula* (Than and McDonald 1973). Focal hepatic necrosis has been described in *A. stuartii* (Barker *et al.* 1978). Hepatocellular damage may be assessed by: a) a decrease in plasma albumin concentration (since the half life of albumin in the circulation is about 20 d in man (Whitby, Percy-Ribb and Smith 1980), only chronic disease would be indicated); b) an increase in the concentration of the liver aminotransferases, alanine aminotransferase (ALT) and aspartate aminotransferase (AST).

It is difficult to extrapolate responses from one species to another. For example, while *Trichosurus vulpecula* has a low resistance to the nitrogen mobilizing activity of corticosteroids (Than and McDonald 1974a, 1974b), within the macropods some species, the Red Kangaroo, *Megaleia rufa* and the Quokka, *Setonix brachyurus*, are highly resistant to these glucocorticoid actions (Griffiths, McIntosh and Leckie 1969; McDonald and Bradshaw 1981), while the Tamar Wallaby, *Macropus eugenii* is more responsive (Cooley and Janssens 1977; Janssens and Hinds 1981).

#### *Animal Problems*

Analysis of blood sampled from animals captured in the wild is compounded by effects that may be induced by the trapping and handling procedures used. Animals are usually subjected to a standard period of acclimation in the laboratory before sampling (Newson 1962; Barnett 1973; Cheal, Lee and Barnett 1976) or bled in the field when the traps were checked (Lee and Brown 1970; Maclean and Lee 1973) but the

effect of trapping and handling was not considered.

In the Australian Bush Rat, *Rattus fuscipes* (Waterhouse), levels of corticosteroids were similar whether bled on release from the trap or after 3d laboratory confinement (J. L. Barnett, unpublished data) but samples taken in the field were considered to reflect more accurately the nutritional status of this species. Short term deprivation of food did not result in increased levels of free fatty acids whereas laboratory held animals showed a marked response to diet by increasing their plasma lipid levels (Middleton 1976).

Handling-induced stress may have delayed effects on blood constituents. In White-tailed Deer (*Odocoileus virginianus*) the stress of handling solely by physical restraint caused, 24 h later, marked changes in many blood constituents similar to those induced within a few minutes by handling with the aid of the drugs phencyclidine or promazine (Seal *et al.* 1972); decreases were observed in haemoglobin concentration, haematocrit, red blood cell count, fibrinogen and total serum protein, while increases occurred in some serum enzymes associated with tissue damage. Such problems can be overcome by analysis of the data to measure the effect of handling induced stress. For example, Franzmann (1972) found that rectal temperature, haematocrit, cholesterol, glucose, haemoglobin, total plasma protein and calcium of Bighorns (*Ovis c. canadensis*) were influenced by the level of excitability, which he measured from the heart and respiratory rates and physical struggle.

There was an interaction between the level of excitability and whether the individuals were captive or wild. This approach, namely the familiarity of the subject with the handling procedures, was used by Barnett, How and Humphreys (1979a) to look for trapping effects on blood constituents from *T. caninus*. They partitioned the haematocrit data according to first ever or third bleed and the former also into trap naive and trap experienced individuals, but could detect no effect of trap or handling experience on haematocrit.

Additionally the levels of plasma glucose were similar to those of *T. vulpecula* sampled using the same methods at the same site and time. The glucose levels of these *T. vulpecula* were similar to "normal" laboratory values (Than and McDonald 1974) but much lower than those from deliberately stressed animals (Parsons, Guiler and Heddle 1971). As the levels of other blood constituents in *T. caninus* changed seasonally they could not be evaluated for the effects of trapping and handling (Barnett, How and Humphreys 1979b).

#### INTERPRETATION OF CONDITION CRITERIA

Given that the problems discussed above can

be solved and accurate levels of the various blood constituents determined, what interpretation is to be placed on the blood values; what do such measures mean in terms of individual condition? Clinically an abnormal level of a physiological parameter (e.g. haemoglobin concentration, globulin, free corticosteroid) is considered indicative of illness that may result from a multitude of causes. The abnormal level is related to all the signs and symptoms, perhaps followed by further tests on more specific substrates, to identify the specific cause of the malady. However the original abnormal levels were sufficient in themselves to deduce some malfunctioning in the individual who, whether human or stock, probably presented with some categorized illness or loss of condition in the clinical sense. In a wild animal illness will be associated with poor performance in some aspect of the individual's biology; this will increase the risk of death or lower its reproductive performance and so reduce its fitness (condition in an ecological sense). Obviously there is overlap between these aspects of condition; poor nutrition results in poor clinical condition, but in humans may result in suckling induced amenorrhoea which has demographic implications. Analysis of physiology and demography of natural populations aims to detect such interactions.

In a study of Rocky Mountain Bighorn and California Bighorn Sheep, habitat differences, which were mainly attributable to different forage types, had greater influence on blood constituents than did condition or subspecific status and, as discussed above, excitability of individuals at sampling was the prime cause of variation. In those animals with known forage, blood urea nitrogen was positively related to forage protein content and glucose was also elevated (Franzmann 1972). No analysis was conducted to derive differences between the sexes. In ponies chronic fasting caused various changes in blood constituents which returned to pre-fasting levels within six days on refeeding. The most pronounced effect was lipemia, as all plasma lipid components increased during the fast as the metabolism changed to the use of fat reserves (Baetz and Pearson 1946). Baetz and Pearson suggested that those components remaining unchanged were useful to determine the disease process as distinct from the adequacy of nutrition.

In the field, however, we are interested in changes in parameters on both temporal and spatial dimensions as indicators of performance. Weather *per se*, as opposed to seasonality, does not appear to be an important consideration. For example six weather factors were of no value in predicting changes in the haematological values of Mule Deer (Anderson, Medin and Bowden 1970). Changes in variables of potential use as condition indices are not directly interpretable.

For example Edozien and Switzer (1977) fed rats different levels of energy, fat and protein. Both haemoglobin and haematocrit increased with protein intake with no suggestion of a cut-off point up to 50% protein in the diet whereas rats fed low (5%) or high (21%) fat diets had lower haemoglobin and haematocrit levels than those fed a diet with intermediate fat content. Low energy intake reduced haematocrit but had no effect on haemoglobin. While this study confirms that anaemia is a regular feature of protein deficiency, it may be complicated by deficiencies of specific haemopoietic agents such as iron and folacin (Edozien and Khan 1968; Viteri *et al.* 1968). In dogs chronic protein deficiency results in low albumin levels while globulin levels remain essentially unaltered; several weeks of adequate diet were required to restore the levels to those before the imposition of protein deficient diet. Globulin levels marginally increased mainly due to elevated alpha globulin levels which were associated with elevated levels of plasma lipids (Zeldis *et al.* 1945). Using an efficient Latin square design, Fonnesebeck and Symons (1969) showed that, in horses, blood urea nitrogen was directly related to dietary nitrogen, apparent nitrogen absorbed and urinary nitrogen excretion, whereas plasma protein increased with dietary nitrogen but there was more within than between treatment variation, so the measure is not an efficient criterion for evaluating protein requirements in horses. Plasma sugars were positively related to dietary intake and plasma cholesterol rapidly responded to diet.

In phalangers the only analysis of animals in different clinical condition was conducted on *T. vulpecula*. Animals brought into the laboratory in clearly bad condition, resulting from three days of inadequate food and water, overcrowding and poor ventilation, were compared with animals in good clinical condition. Animals in poor condition were thin, depressed and dehydrated with sunken eyes and rough dry fur and often with bite wounds, while those in good condition had good pelage, no obvious bite wounds and were well muscled and fat. Of all the parameters measured only sodium in females showed significant (our analysis by ANOVA) differences between condition status, even free corticosteroid levels were not statistically separate despite being twice the concentration in poor condition males than in those in good condition; Presidente and Correa (1981) attributed the trends in the differences to dehydration. The resilience of these possums to acute deprivation is encouraging in that the rapid handling of animals in the field would not be expected to cause substantive changes before blood was taken.

Overt differences in body weight and fat reserves between populations of White-tailed Deer (*O. virginianus texanus*) were not reflected in the blood picture but poor condition was

associated with elevated blood urea nitrogen (Kie, White and Drawe 1983), contrary to the findings in many species (Fonnesebeck and Symons 1969). These observations led Kie, White and Drawe (1983) to conclude that post mortality blood chemistry and haematology were of limited additional value to deer management in assessing physical condition in field situations.

In *O. virginianus* serum cortisol, its response to ACTH stimulation and adrenal weights were not related to population density. There was therefore no evidence for a simple density-dependent elevation in adrenal corticosteroid secretory activity in healthy, well-fed White-tailed Deer from a population with rapidly increasing numbers (Seal *et al.* 1983).

### THE APPLICATION OF CONDITION ASSESSMENT TO POSSUM POPULATION BIOLOGY

The previous section indicates that while there are numerous parameters available to assess condition there are also numerous practical problems in their application and theoretical problems in their interpretation. Also, ecological studies of possums, or other species, would rarely have condition assessment as a specific aim, and it is usually only with hindsight that its importance is realised. For these reasons it is not possible to make generalised statements relating condition with specific population parameters, and instead, we will show which aspects of condition can relate to population biology within the few studies that have been done; a table of source references is in Appendix I.

#### *T. vulpecula* in New Zealand.

Many studies on *T. vulpecula* in New Zealand used Bamford's (1970) equations to estimate the fat reserves in other populations which were aged by counting cementum rings in the teeth after the method of Pekelharing (1970). Bamford (1970) measured several fat depots in *T. vulpecula* in New Zealand and related them to body weight. He derived equations, accounting for much of the variation, relating total body fat (f) to body weight (W) as a percentage of standard body weight (Ws):

$$\text{for males } f = -9.7 + 0.33 (100 W/W_s);$$

$$\text{for females } f = -15.9 + 0.41 (100 W/W_s).$$

He considered that the form of the equations would be generally applicable although the constants may vary between populations. This is pertinent in that ecologists are primarily interested in relative changes in condition and, as yet, cannot use any single measure of condition to quantify fitness.

Nineteen populations of *T. vulpecula* were examined by Boersma (1974) in the Hokitika River catchment in New Zealand using samples collected in September through December from

areas where some possum control operations had been conducted. He obtained four interrelated condition indices; calculating from his data the density of possums (DI), indexed from faecal pellet counts, was inversely related to both of his pooled index of condition and to the estimated fat reserves as estimated from Bamford's (1970) equations:

$$\text{pooled condition} = 5.1 - 2.40 \log(\text{DI}), r = 0.35, P < 0.01$$

$$\text{female fat reserves} = 23.5 - 1.35 \log(\text{DI}), r = 0.34, P < 0.05$$

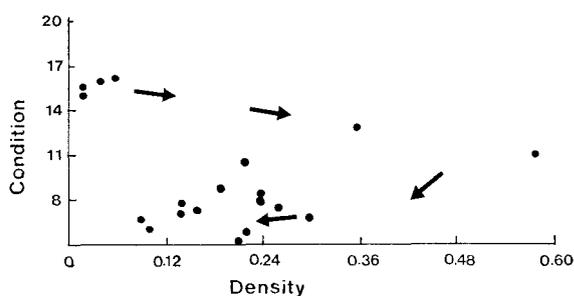


Fig. 1. The relationship between population density and percentage fat reserves of female *T. vulpecula* in the Hokitika River catchment, New Zealand. The data were extracted from Boesma (1974). The index of density is based on faecal pellet counts and the fat index is based on Bamford's (1970) equations.

The data show two outliers having both high density and condition (Fig. 1). Points in the upper left of Fig. 1 were from populations having recently colonised the areas, while most of the other points were from areas of well established populations. The order of the points suggests a possible trajectory of population establishment, indicated in Fig. 1; areas of recent colonisation have low populations with good food resources, the density increases while adequate food is available and condition is maintained. Eventually food resources are over exploited and condition and population density decline to a level where the population is in balance with the supply of food. The high density with good condition state would be of short duration and therefore should be difficult to detect.

Fraser (1979) compared three populations of *T. vulpecula* from Copeland Valley, Westland and considered that density was indicated by the proportion of possums killed per bait laid. Females in high density areas (lowland) matured later, were smaller as adults, and had less abdominal fat, than mid to low density (upland) populations.

The major New Zealand study has been in the Orongorongo Valley where *T. vulpecula* have been monitored in two areas for more than ten years (Kean 1959, 1967, 1971, 1975; Crawley

1970, 1973; Bell 1981). The two areas differed considerably in their demographic characteristics within years (Table 1) and there was marked between year variations within areas (Table 2). Bell (1981) considered that years of poor food availability reduced the growth rate which delayed the onset of breeding and that females in poor condition (low relative body weight) bred less successfully. He suggested that females, where possible, lay down fat reserves in autumn and early winter and utilize them in late winter and early spring when the pouch young are growing fast and the demands of lactation are highest. Females unable to mobilise fat reserves in this way either fail to breed or are unable to sustain young through the winter.

Females can breed in their first year but the young rarely survive (Bell 1981). In the wild such early breeders, with 4-6 month old pouch young, are often underweight, mildly anaemic and hypoproteinaemic; although in the laboratory such pouch young respond to feeding by a marked increase in weight, in the wild they would be rejected (Presidente and Correa 1981). An inability to sustain young occurs also later in life: in the Orongorongo Valley females showed a marked lowering in birth rate and survival of pouch young between the last two years of life (Bell 1981), indicating long term loss of condition prior to death.

In the Orongorongo Valley the dates when young were born and lost (died) are respectively directly and inversely related to female weight (Bell 1981). Although not discussed by Bell, calculation shows that these relationships result in the average median date that pouch young were lost in the Orongorongo Valley over the period 1966 to 1975 was 19 August (S.E. = 3.7 days). This remarkable consistency between years of markedly different demographic performance suggests that a factor operating on a strict seasonal basis, and independent of the processes discussed by Bell, is influencing the death of pouch young.

Breeding data separated into those individuals rearing young, losing young, and not breeding show similar trends in both area A and B of the Orongorongo Valley (Fig. 2). Breeding success was related to the weight of adult females, however details of the weight changes differed between the two areas. Weight changes were more marked, and occurred a season earlier in area B than in area A for the subset successfully rearing young (Bell 1981).

Population density in the Orongorongo Valley correlates well with various indices of the previous year's breeding success but not with indices of the current year (Table 2). Breeding success is correlated with indices of food availability, hence the data are consistent with the proximate cause of population density being food availability.

Table 1. Differences in demographic characters between populations of *Trichosurus vulpecula* from areas A and B in the Orongorongo Valley, New Zealand. Data are abstracted from Bell (1981). p.y. = pouch young.

CHARACTERISTICS (between areas)	Area A	Delta	Area B
Mean birth data: successful rearing	May 13		May 6
failed rearing p.y.	June 1	p<.001	May 14
Birth rate		A=B	
Survival rate p.y.	58%	A>B <.05	42%
Colour morphs; grey:black (g:b)	60:40	<.05	46:54
breeding success		A=B	
age first breeding		g=b	
Yearlings; birth rate	8%		0%
p.y. reared	0%		0%
2 year olds; birth rate	72%	A>B <.05	57%
p.y. reared	34%		0%
Adults; birth rate	81%	B>A <.01	93%
p.y. reared	62%		44%
Yearly heterogeneity: birth rate	<.01	A>B	N.S.
survival p.y.	<.001	A>B	N.S.
Adult females: weight (kg)		A=B	
without p.y.	2.13	A=B	2.2
losing p.y.	2.19	A<B <.04	2.22
rearing p.y.	2.34	A=B	2.38
% standard weight	105.7	A>B <.001	98.2
without p.y.	98.8	A=B	94.3
losing p.y.	101.5	A>B <.001	95.9
rearing p.y.	105.9	A>B <.001	101.7
Seasonal weight variation (%)	0.9	A<B	6.3
Mean annual weight changes (winter)	up or down		always down

Table 2. Annual variation in demographic parameters of *Trichosurus vulpecula* from the Orongorongo Valley, New Zealand. Data are abstracted from Bell (1981). All relationships are statistically significant at  $\alpha < 0.05$ .

Weights of both sexes respond similarly within years.
The timing (season) of weight change differs between years.
Mean percentage standard weight for autumn: inversely related to date of birth (P=.01) directly related to % adults with pouch young (P=.009)
Mean percentage standard weight for winter directly related to: % adults rearing pouch young (P=.022) mean age pouch young lost (P=.02)
Mean weight adults in autumn directly related to mean weight of yearlings in autumn
The number of adults known to be alive the following year is: inversely related to median date of birth (P=.006) directly related to % adults having pouch young (P=.023) directly related to mean autumn weight of adult females (P=.01) directly related to mean winter weight of adult females (P=.018)
The numbers known to be alive in the current year are not related to any of the above four parameters (P=.67 to .95)
The annual crop of Hinau fruit is directly related to: median date of birth (P=.012) % adults having young (P=.0018) mean annual weight of adult females (P=.008) mean winter weight of adult females (P=.0008) mean autumn weight of yearlings (P=.029) total seedfall (P=.041)

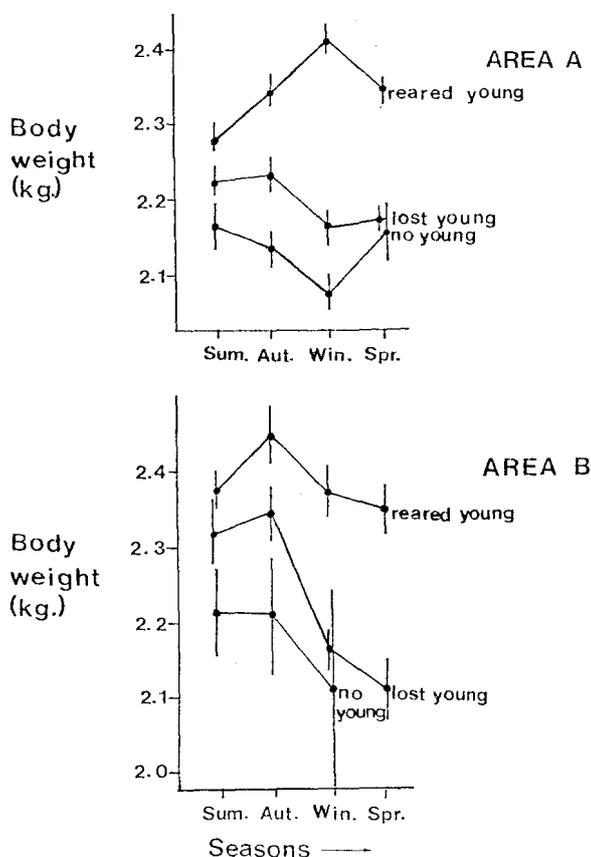


Fig. 2. Seasonal changes in weight of three reproductive classes of female *T. vulpecula* from two areas in the Orongorongo Valley, New Zealand.

While there are no data from the Orongorongo Valley possums directly pertinent to the scheme derived from Boesma's data (Fig. 1), the trends in both data sets are explicable in terms of food resources. It should, however, be noted that changes in condition, judged by body weight, may not be indicative of low nutrient availability. For example *Rattus fuscipes* (Waterhouse) in the wild exhibited loss in body weight and loss of weight in a number of organs in winter, but so did captive animals provided *ad libitum* with food and water (Stewart and Barnett 1983).

### *T. vulpecula* in Tasmania.

Hocking (1981) studied Tasmanian populations of *T. vulpecula* inhabiting forest which had recovered for different periods (0-60+ years) following fires. Overall, his data are consistent with those of Bell (1981) from Orongorongo in that they suggest food resources, both qualitative and quantitative, limit carrying capacity and regulate  $r$ . Populations inhabiting forests of different age (post fire) exhibited wide variation in demographic parameters. The condition index, juvenile survival, density, fecundity and growth rate increased from 1 to 4-6 year old forest following which all parameters, save the latter two, declined to a roughly constant level in forest aged

between 8-16 and 80+ years. Fecundity and growth rate declined continuously in forest aged greater than 4-6 years (Fig. 3).

Both sexes reached reproductive maturity later in older aged forest. After maturity the incidence of breeding and the survival of dependent young were lower in recently burnt habitats. Hocking calculated that the differences amounted to about a 40% reduction in the intrinsic rate of natural increase ( $r$ ) and this is 70% of the variation expressed over the entire geographic range of *T. vulpecula*. It should be noted, however, that the  $r$  values were calculated without direct knowledge of longevity or age specific fecundity.

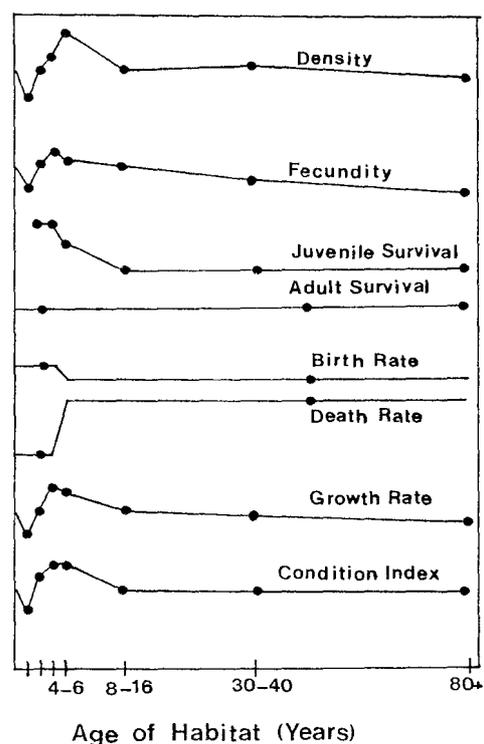


Fig. 3. Schema showing relative levels of parameters in *T. vulpecula* populations inhabiting forest in Tasmania which had recovered from fire for various periods ("age of habitat"). Redrawn from Hocking (1971).

### *T. vulpecula* and *T. caninus* in Australia.

In Australia only one study on phalangers is comparable in duration to that of the Orongorongo Valley population. How (1972, 1976, 1978, 1981) examined populations of *Trichosurus vulpecula* and *T. caninus* at Clouds Creek in north-eastern New South Wales between 1967 and 1972. These populations were then followed until 1976 to monitor both their demography and physiology in the field (Barnett, How and Humphreys 1979a, 1979b, 1982; Presidente *et al.* 1982). It is notable that these two species cannot be separated on cranial or enzymatic criteria (J. A. Kerle, pers. comm.), but they are recognizable in life and by numerous biological

differences. For example *T. caninus* breed at a later age (three years compared to one year, How 1976) and have persistent corpora albicans (Smith and How 1973). *T. caninus* probably excludes *T. vulpecula* from areas of closed and tall open forest (How 1972).

The single study area at Clouds Creek included a number of vegetation types (Specht's 1970 classification). *T. caninus* was mainly confined to closed and tall open forest while *T. vulpecula* occurred mainly in open forest and grazed woodland but was found also in pine plantations (Barnett, How and Humphreys 1976). The *T. caninus* population was subdivided into those in "preferred" and "peripheral" habitat using the criteria that an individual ever trapped (during its entire trap history of up to ten years) outside closed and tall open forest was assigned to the peripheral category, otherwise to the preferred habitat category.

After correction for age and sex related differences, significant seasonal changes were found in: *T. caninus* for plasma glucose and protein concentrations, haemoglobin concentration and red blood cell count; and in *T. vulpecula* for haemoglobin concentration (Barnett, How and Humphreys 1979a). Adult *T. caninus* had higher mean levels of body weight, haematocrit and haemoglobin concentrations, but lower plasma lipid levels and red blood cell counts than adult *T. vulpecula*. Seasonal variation in the measured parameters was greater in the more *K*-selected species, *T. caninus*, than the more *r*-selected species, *T. vulpecula* (Barnett, How and Humphreys 1979a).

Comparison of these two species from preferred and peripheral habitats (defined above) showed that habitat had a pronounced effect on *T. caninus*. Of the seven parameters measured, six (body weight, red blood cell count, haematocrit, and plasma lipid, plasma protein and haemoglobin concentrations) were higher in individuals from the peripheral habitat where it overlapped in range with *T. vulpecula*. Plasma lipid concentration of *T. vulpecula* was the same as in peripheral habitat *T. caninus*, but differed between habitats in *T. caninus* (Barnett, How and Humphreys 1979b).

Four parameters exhibited significant seasonal variation in preferred-habitat *T. caninus*, three in peripheral habitat *T. caninus* and one in *T. vulpecula*. However the pattern of seasonal change in peripheral habitat *T. caninus* was more similar to that in *T. vulpecula* than to that in preferred habitat *T. caninus*. It was suggested that there was a physiological shift in peripheral habitat *T. caninus* towards the pattern found in the more *r*-selected *T. vulpecula* (Barnett, How and Humphreys, *ibid*).

No differences in the haematological parameters, as indices of condition, were detected

between resident and dispersing *T. caninus*. However, this may not be unexpected as their reproductive strategy is one of high parental investment (cf. lower investment in *T. vulpecula*) and dispersal should occur when the animals are fit (in good condition) with a high probability of survival. Those female *T. caninus* which lost a pouch young, and failed to maintain another within the same year, had lower haematocrits and plasma lipid concentrations than females in all other reproductive categories, suggesting a poorer condition. Haematocrit was also higher in lactating females with dependent or semi-dependent young than in non-lactating females (Barnett, How and Humphreys *ibid*).

At autopsy, organ weights were determined and calibrated against known age/weight individuals (Barnett, How and Humphreys 1981). Body, kidney, spleen and male liver weights were greater in peripheral habitat animals, while female adrenal glands were heavier in preferred habitat females. Adrenal gland weight in preferred habitat females was only 16% more than males and peripheral habitat females despite most having pouch young at the time. This differs from *T. vulpecula*, wombats and kangaroos where the female adrenal weight is nearly twice that in males. Furthermore the female adrenal enlarges during lactation in *T. vulpecula* due to an increase in the X-zone (Bourne 1934; Tyndale-Biscoe 1973).

As there were no clear demographic differences between *T. caninus* from the preferred and peripheral habitats, Barnett, How and Humphreys (1982) convolved a range of data to explain the observed interhabitat differences in the number of corpora albicans per female per year; there were more in the peripheral habitat. From the available evidence (summarized in Table 3) they considered four hypotheses but discounted the first three:— 1) fewer females in peripheral habitat became pregnant at their first oestrous and returned to oestrous; 2) females in peripheral habitat had more young; 3) more females in peripheral habitat lost pouch young and returned to oestrous. Having discounted these they considered the possibility of behavioural differences between possums in the two habitats.

They showed that the sex ratio of pouch young, but not the adults, differed between the habitats which suggested differences in dispersal between habitats which was, on average age, 11 weeks later in the preferred habitat. As retention of young in the mother's home range may suppress the mother's subsequent breeding (How 1981) the longer retention of young in preferred habitat should result in suppression of breeding. This was consistent with the elevated free steroid levels found in preferred habitat females (Presidente *et al.* 1982) which are indicative of stress.



Table 4. Summary of the differences recorded between *T. caninus* inhabiting adjacent tall open and closed forest (preferred habitat) or other forest types (peripheral habitat) at Clouds Creek, northeastern New South Wales. After Barnett, How and Humphreys 1982.

Class of Observation	Preferred habitat > or < than peripheral habitat	Parameter
Gravimetric	<	Body
	<	Kidney
	<	Spleen
	<	Liver in male
	>	Adrenal in female
Demographic	>	Sex ratio of pouch young
	<	No. of corpora albicans $\text{♀}^{-1}\text{y}^{-1}$
Genetic		Phenotypic distribution of transferrin
Behavioural	>	Age of dispersal of young
Endocrinological	>	Free corticosteroid in female
Haematological	<	Erythrocytes
	<	Haemoglobin concentration
	<	Haematocrit
	<	Plasma protein
	<	Plasma lipid
	Parasite burden or prevalence	<
<		<i>Adelonema trichosuri</i>
<		<i>Bertiella trichosuri</i>
<		<i>Ixodes</i> spp.
<		<i>Trichosurolelaelaps dioxa</i>
<		<i>T. crassipes</i>
>		<i>Paraastrostrongylus trichosuri</i>
Seasonal variation	>	Haemoglobin
	>	Erythrocyte count

No difference observed in: plasma glucose; heart weight; testis weight; epididymis weight; prostatic urethra weight; age distribution; adult sex ratio; size of home range; number of pouch young per female per year; mortality of pouch young; timing of first birth.

examined showed differences: demographic, genetic, gravimetric, behavioural, endocrinological, haematological, parasitological. Such differences pose considerable problems to the definition of study populations and, in particular, the establishment of control populations in experimental ecology (Barnett, How and Humphreys 1982).

#### *Petauroides* (= *Schoinobates*) *volans*

A population of the Greater Glider, *P. volans* (Kerr), was studied near Tumut in New South Wales (Smith 1969; Tyndale-Biscoe and Smith 1969a, 1969b; Marples 1973). This species is polyoestrous and monovular. Breeding commences in March and the females reach sexual maturity in their second year at about 1 kg and produced a single young. Adults of each sex appear to be more regularly spaced than random. The gliders show a consistent pattern of weight distribution throughout the year; the modal weight was 1.25 kg in all seasons save winter when it fell to about 1.15 kg. The sex ratio between birth and six months is parity, shifting to 0.39 in immature and mature animals. This shift in the sex ratio seems to occur when the young disperse to establish their own territories. From 25 to 40% of adult females had no pouch young in summer and bore no evidence of having had one. A sample collected in June showed 26% to be anoestrous. Tyndale-Biscoe and Smith (1969b) analysed the data and considered that the number of breeding females equalled the

number of mature males in the area. Non-breeding females were of similar weight and linear dimensions so appear to be in the same overt condition; hence they suggested that unknown behavioural factors, rather than changes in condition, regulated breeding. They did not pursue the matter further; however presumably male density is dictated in some way by available resources and once fixed this determines the density of breeding females. In this sense the females have little impact on the population density. It is unfortunate that aspects of condition of males were unreported in this study. They did, however, show that animals removed to areas already populated by *P. volans* survived mostly for only a week and showed progressive loss of up to 25% of the initial weight. It is improbable that these enforced immigrants exerted appreciable foraging pressure as at their mean density (0.8 gliders  $\text{ha}^{-1}$ ) they consumed only about 6 kg dry matter  $\text{ha}^{-1}\text{yr}^{-1}$  (Marples 1973).

#### *Pseudocheirus peregrinus* in Victoria

This Ring-tail Possum has been studied in inland scrub at Warramate (Thomson and Owen 1964) and in coastal *Leptospermum* thickets at Sandy Point (How *et al.* 1984). In Victoria *P. peregrinus* have, judging from the corpora lutea, low pouch young mortality (Hughes, Thomson and Owen 1964) and this was confirmed from a longitudinal study (How *et al.* 1984). Males at Warramate were lightest during late spring to early summer (when they exhibited testicular

regression) and heaviest in autumn and winter — an annual weight variation of up to 25%. Females at Warramate lost weight in late winter, spring and summer, associated with the development and feeding of young. There were large between-year differences in weight during the same season (100 g) but this did not influence litter size at Warramate. The animals appeared to move little and one plot from which animals were removed was not occupied by neighbouring individuals over a period of six months (Thomson and Owen 1964) or a year (How *et al.* 1984).

At Sandy Point, by contrast, both sexes were heaviest in January. Females showed marked weight loss over summer and were lightest in May at about the time breeding was at a peak. Weight increased during the time young were developing. Males lost weight between late summer and mid winter and this weight loss coincided with reduced male survival after weaning (6 to 12 months) and from 18-24 months (How *et al.* 1984). *P. peregrinus* exhibited no seasonal change in free corticosteroid concentration [CS] (our unpublished data).

At Sandy Point primiparous females bred later (about five weeks) than previously parous females (How *et al.* 1984); this may be a phenomenon similar to that seen in Bell's (1981) *T. vulpecula* where low body weight was associated with primiparous females, delayed breeding and lower survival of pouch young.

#### **Wyulda squamicaudata**

The few data available for this species show no overt changes in body weight or fur condition over the year (Humphreys *et al.* 1984). However, marked seasonality occurs in plasma protein and albumin concentrations with both declining during the dry season and elevated during the wet season (November to April). Similar variation occurred in free corticosteroid levels with the highest values in the late dry season [June-October] at which time females are carrying pouch young.

### **FACTORS AFFECTING CONDITION IN PHALANGERS**

#### **Genetic influences**

Of the three species assigned to *Trichosurus* only *T. vulpecula* from north Queensland and *T. arnhemensis* from Barrow Island off Western Australia can be separated by their genetic relatedness using 13 loci. Other populations of *T. arnhemensis* and *T. vulpecula* and *T. caninus* cannot be separated from each other (G. M. McKay and J. A. Kerle; pers. comm.). However at specific loci regional populations may differ substantially from each other. *T. vulpecula* show polymorphism at the serum amylase locus; high proportions of the A gene occur in the southwest of Western

Australia and in South Australia, except on islands and peninsulas, and low proportions of the A gene occur in Victoria and New South Wales (Hope and Finnegan 1970). The study of *T. caninus* (referred to above) detected numerous differences in many parameters between possums living in contiguous, but different, forest types. These were associated with differences in the genotypic distribution of a transferrin polymorphism. This enzyme is known to be associated with aspects of fertility and sex ratio in eutherians, differences established also for *T. caninus* from the two habitats (Barnett, How and Humphreys 1982).

*T. vulpecula* occurs naturally as melanic and grey morphs in Tasmania. Both mainland and Tasmanian possums were introduced into New Zealand. In Tasmania and parts of New Zealand the melanic form is associated with wet forests and the grey form occurs in drier areas. This suggested to Kean (1971) that there may be genetic linkage between the colour morphs and adaptation to humid conditions. In the Orongorongo Valley, New Zealand, two populations (A and B) differed in their proportion of melanic females (40% and 54% respectively). Whilst the populations differed in most aspects of their demography, no differences between the colour morphs were detected in any demographic measure examined (birth rate, survival of pouch young, age specific breeding success (Bell 1981)).

By contrast Williams and Turnbull (1983) compared *T. vulpecula* populations from North Island (Wanganui) and South Island (Haupiri) which were respectively of agouti and melanic colour phase. Using controlled environment chambers they examined, under two temperature conditions, aspects of nutrition, thermoregulation and water balance. The Haupiri possums were considerably heavier (1.25x) than their northern counterparts, consistent with Bergmann's rule. The data showed that individually the possums had similar food intake and water turnover, but these parameters showed considerable differences when expressed in units of individual metabolic size. They concluded that the large size of Haupiri individuals confers advantage during fasts enforced by bad weather, while the small size of Wanganui possums is advantageous in periods of prolonged rainfall deficiency. It is not known whether these physiological traits are related to the coat-colour polymorphism (Williams and Turnbull 1983). Note that no ecological differences were found between the colour morphs in the Orongorongo population.

#### **Feeding and Nutrition**

The basal metabolic rate (BMR) of marsupials is generally about 30% lower than in eutherians of similar size (Dawson and Hulbert 1970; but see McNab 1983). However, the BMR in both taxa is

related to their trophic habits. The phalangers occupy two trophic groups, namely, arboreal folivores (*Trichosurus* spp., *Phalanger* spp., *Wyulda*, *Pseudocheirus* spp. and *Petauroides*), and arboreal omnivores (*Gymnobelideus*, *Petaurus* spp., *Cercartetus* spp., *Acrobates*, *Tarsipes* and *Burramys*). Arboreal folivores have low BMR irrespective of whether they are marsupial or eutherian, namely 59% and 53% of Kleiber's (1961) standard eutherian value; this value for marsupial omnivores is about 70% (McNab 1978).

It seems that marsupials similarly have low maintenance requirements for nitrogen and energy. *T. vulpecula* has maintenance requirements for nitrogen much lower than eutherians (203 mg kg<sup>-0.75</sup> d<sup>-1</sup> on a dietary basis and 189 mg kg<sup>-0.75</sup> d<sup>-1</sup> on a truly digestible basis) and probably low maintenance energy requirements (Wellard and Hume 1981). The nitrogen requirements of *T. vulpecula* are similar to these for most macropods (the only other marsupials examined), but the Red-necked Pademelon, *Thylogale thetis*, has maintenance requirements equal to or greater (530 mg kg<sup>-0.75</sup> d<sup>-1</sup>) than many eutherians (Hume 1977). Hence the nitrogen requirements of *T. vulpecula* should not be generalized to other phalangers.

The chain of consequences of low BMR to the requirements of marsupials for water, energy and protein have been discussed by Hume (1982) and they are of particular relevance here in relation to the environmental tolerances of folivores compared with omnivores.

The food requirements in the field have not been explicitly determined for any phalangers, but Marples (1973), from an analysis of stomach contents, concluded that the Greater Glider, *Petauroides volans*, required about 6 kg dry matter ha<sup>-1</sup> yr<sup>-1</sup> to sustain the population near Tumut in New South Wales. This may be an underestimate as captive individuals consumed 46 g dry matter per day compared with Marples' estimate of 20 g dry matter per day (Hume 1982). This difference does not materially alter Marples' suggestion that food was unlikely to be limiting to the population, one which Tyndale-Biscoe and Smith (1969b) had suggested was limited by behavioural feedback. While either of these food demands is low, the population densities of *P. volans* (0.8 ha<sup>-1</sup>) were not dissimilar to those for populations of other species of phalanger inhabiting tall forest (How 1978).

In New Zealand, populations of *T. vulpecula* reach much higher densities than in Australia and when establishing themselves in new areas follow typical colonisation curves: a rapid increase in density far in excess of the source area followed by a decline to densities close to those of the source area (Tyndale-Biscoe 1981). The following discussion is pertinent to the carrying capacity of forest for phalangers.

Most of the large phalangers rely heavily on *Eucalyptus* foliage for food. Eucalypt leaves are of low nutritive value and contain many toxic secondary products. In an analysis of eucalypt leaves eaten by Koalas, *Phascolarctos cinereus*, Cork (1981) was unable to find any seasonal differences in the level of any of the constituents although in captivity they select younger leaves which differ in many aspects from older leaves and contain higher levels of crude protein and phosphorus and lower levels of fibre and lignin (Ullrey, Robinson and Whetter 1981). It is possible that despite the apparent food plenty in forests, folivores may find inadequate new growth to eat only preferred food; the animals may then be forced seasonally onto food that is both less nutritious and containing more secondary substances. The next section deals with possible consequences.

Freeland and Winter (1975) found that wild *T. vulpecula* spent 66% of the time feeding on mature *Eucalyptus* spp. leaves. Caged possums fed three species of *Eucalyptus* ate barely enough to support their standard metabolic rate but sampled the species offered. If fed a single food species they initially ate only half as much as when fed three food species but gradually consumed more. *Eucalyptus* leaves contain volatile oils and phenols which are toxic and induce microsomal detoxification when eaten. Hence, Freeland and Winter (1975) argued that possums could not obtain all their food requirements from eucalypts due to the toxins and have to consume non-eucalypt food in order of subsist; thus on their hypothesis the possum population is limited indirectly by the presence of toxic secondary compounds in its major food item and by the availability of minority food items which are not toxic or less toxic. They suggest that the data for *T. vulpecula* from New Zealand are consistent with their hypothesis and that trees which have survived there are less attractive (more toxic) to the possums.

This thesis of Freeland and Winter (*ibid*) has particular significance to the larger phalangers in general: all are arboreal folivores so they rely on plants with very high apparency (*sensu* Feeny 1976) in which chemical defence may be expected to be most highly developed (Rhoades 1979). Freeland and Winter's hypothesis has been challenged on several grounds in more recent work. Eucalypts are not necessarily the most important dietary item and species with high alkaloid concentrations may be consumed almost exclusively (J. A. Kerle, pers. comm.). Furthermore, animals may evolve to cope with toxins; this is illustrated by the 100-fold difference in the tolerance of *T. vulpecula* to monofluoroacetate (1080) in Western Australia where it occurs commonly in plants, compared with the tolerance shown in eastern Australia where 1080 is absent from plants (King, Oliver and Mead 1978; McIlroy 1982). Although toxins may play a

role in food selection, it is digestibility and fibre content which lead to selection of a varied diet in *T. vulpecula* (Kerle 1984).

Strong chemical defence, of the type indicated by Freeland and Winter and elsewhere (papers in Rosenthal and Janzen 1979), may influence phalanger populations by their impact on available energy, spatially and temporally, as well as by direct effects on fertility, mortality (Rhoades 1979) and density, namely the demographic factors with which we are concerned here. Clearly floristics as well as primary productivity may influence the carrying capacity of forest for phalangers. It should be appreciated that even if these parameters are held constant, plants may show qualitative changes in their defensive repertoire in response to stress of many types (Rhoades 1979; e.g. drought, heat, cold, poor health, nutrients, shading . . .). It follows that forest management practices, more subtle than the widespread practice of clear-felling phalanger habitats, may have unexpected effects on the populations contained. This is supported in the study by Braithwaite, Dudzinski and Turner (1983) which showed high correlations between foliage nitrogen and potassium levels and the density of possums.

### Sex Ratio

There has been considerable debate concerning the sex ratio of marsupials since Shield (1962) stated that marsupials having been "released from the major male-biased causes of intra-uterine deaths in eutherians, do not, as a consequence, have a high secondary sex ratio. The ratio is in fact little removed from parity". Caughley and Kean (1964) examined data from seven marsupial species (including *T. vulpecula*) and found no evidence for differential mortality during life in the pouch but found sex ratio bias in *Macropus giganteus* (=canguru; 1.36) and possibly in *T. vulpecula* (1.14;  $0.1 > P > 0.05$ ). Hope (1972) added further data for *T. vulpecula* to those above and found significant sex ratio bias (1.14) and data consistent with differential mortality between the sexes during pouch life. There was no evidence of differential mortality between the sexes during pouch life in *T. caninus*, either within a population (How 1976), or between habitats when greater breeding suppression occurred in one habitat associated with retention of a previous young within the mother's home range (Barnett, How and Humphreys 1982).

Considerable male biased mortality occurs during dispersal in *P. volans* (Tyndale-Biscoe and Smith 1979a) and *T. vulpecula* (Bell 1981) but not in *T. caninus* (How 1976) nor *P. peregrinus* (How *et al.* 1984). Such mortality is considered to result from the failure of juveniles to establish themselves in vacant habitat (How 1981, Tyndale-Biscoe and Smith 1969b). No physiological differences could be found between dispersing and resident juvenile *T. caninus* (Barnett, How

and Humphreys 1969b); such differences have not been examined in those species showing dispersal related mortality and in which one may expect to detect overt change in condition.

### Parasites

Acute illness is rarely seen in wild populations: in 1954 *Pseudocheirus peregrinus* (= *convolutor*) suffered a population crash and debilitated individuals with severe scouring were seen during the day hanging from or resting on open branches over much of Tasmania (B. C. Mollison pers. comm. in Thomson and Owen 1964).

Parasites can cause overt loss of condition or death to their host but may also influence the fitness of organisms without overt loss of physical condition. Mice infected with a single species of nematode can be prevented from establishing dominance in a manner that is dose dependent and which does not result in loss of weight (Freeland 1981). Condition (health, vigour) and parasitism are related in a way that may play a role in sexual selection (Hamilton and Zuk 1982). Additionally, challenge from parasites may be influential in determining spatial pattern of individuals at a local scale (Freeland 1977).

Phalangers have rarely been examined for parasites in relation to their ecology. *Wyulda squamicaudata* harboured eight *Salmonella* serotypes in a habitat where a total of 29 serotypes were isolated from it and sympatric *Zyomys argurus*, *Z. woodwardi*, *Dasyurus hallucatus*, *Pseudantechinus* sp., *Pseudomys delicatulus*, and *Rattus tunneyi* (How *et al.* 1983). At Clouds Creek *T. caninus* separated by at most several hundred metres harboured markedly different parasite burdens which were associated with the usage made by individuals of local habitat differences (Presidente *et al.* 1982). These have been discussed in more detail above together with associated changes found in *T. caninus* from the two areas.

### Stress and its related mortality

Like "condition", the term "stress" is used loosely. The operational definition used by physiologists is any nonspecific increase in plasma corticosteroids elicited by any one of numerous stimuli. Even in farm animals little is known of the environmental conditions leading to stress, or the physiological processes by which it results in pathologies (Dantzer and Mormede 1983). Stress may result from physiological and/or psychological causes (Dantzer and Mormede 1983; Dickens 1978), so an animal's response to acute stress such as trapping may depend partly on its previous trap history; for example Than and McDonald (1973) found that the metabolic clearance rate of cortisol was much lower in *T. vulpecula* which were unused to the handling procedures necessary to obtain blood samples, a factor which could probably be explained by a reduction in hepatic and renal blood flow.

Perception may alter behavioural characteristics which are overtly of a more "ecological" nature. As an example the shrew *Sorex araneus* feeding in the presence of a potential competitor, despite it being caged, increased the time spent feeding, and urinating, while decreasing time spent sleeping (Barnard, Brown and Gray-Wallis 1983). Presidente (1982) reported that male *T. vulpecula*, when overcrowded, often fought, became depressed, inappetent and developed profuse watery diarrhoea. They rapidly became dehydrated, anorectic and often died within 3-5 days. They exhibited lymphopaenia (to 5%) and neutrophilia (to 83%), changes similar to those found in male *Antechinus stuartii* before their annual die-off (Cheal, Lee and Barnett 1976). Elevated haemoglobin concentration and changes in plasma potassium and chloride values were consistent with dehydration. A high plasma urea concentration (10.4 mmol/L) was attributed to haemoconcentration and a response to elevated corticosteroid levels (Presidente and Correa 1981). Although the free corticosteroid levels were twice that of healthy individuals, we find that the differences are not statistically different. At necropsy these animals were found to have dehydration, emaciation and gastric ulceration with focal haemorrhage. Colonic intussusceptions and rectal prolapse were also found. When they examined material histologically they found involution of splenic lymphoid follicles, adrenocortical hyperplasia with focal necrosis and haemorrhage. Again these changes are consistent with those found in stressed male *A. stuartii* (Barker *et al.* 1978). Farmed *T. vulpecula* in New Zealand suffer similar stress related conditions (Hutton 1979, Keber 1979). Similar pathological findings were not found in a sample of 57 *T. caninus* from a wild population at Clouds Creek (Presidente *et al.* 1982). Such results suggest that *T. vulpecula* which die without physical damage if caged with *T. caninus* (R. A. How, unpublished observation) would yield interesting data at necropsy.

### CONCLUDING REMARKS

We have identified two main reasons for attempting to obtain indices of condition in field populations:

- (a) Management: condition indices are derived as an aid to predicting population changes and formulating management policy. Most of the work on *T. vulpecula* in New Zealand falls into this category and there is a large body of data to this end on the physiology of rodents in central Europe (Dobrowolska *et al.* 1974, Dobrowolska and Gromadzka 1978, Dobrowolska 1982, Dobrowolska and Gromadzka-Ostrowska 1983).
- (b) Heuristic: to explore the relationship between physiological performance, demographic and evolutionary fitness.

We have drawn together a wide range of parameters which have been used by various people in attempts to derive indices of some aspect of condition. Each has been considered useful by one or more authors but no technique seems acceptable as a general condition index that should become a standard method. While physical indices of condition have provided powerful correlations with demographic performance in some phalangers, we have yet to see experimental work testing the ideas derived from the correlations. These indices seem inadequate in explaining the differences observed between populations and habitats. Physiological indices of condition, which have been so instrumental to our understanding of the natural history of some small marsupials, have as yet been of little value in interpreting phalanger biology. It is apparent from the literature reviewed that most attempts to examine condition have failed to establish criteria for a condition index or to consider the resolution required of an index for it to be useful.

Even for mammals as a whole there is a marked paucity of information on the physiological responses to environment of natural populations. Nonetheless it is clear from the data for *T. caninus* at Clouds Creek and *Melomys cf. burtoni* in the Kimberley Region (W. F. Humphreys *et al.*, unpublished data), that a number of measures are highly sensitive to minor changes in locality and discriminate between seasons and between the sexes. However it has not been possible to relate these parameters simply to measures of demographic performance.

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## APPENDIX 1

Available sources of information on blood constituents of phalangers. Capital letters denote references concerned with natural populations and lower case letters those with captive animals.

	<i>T. vulpecula</i>	<i>T. caninus</i>	<i>P. peregrinus</i>	<i>W. squamicaudata</i>
Haematology	A,b	A	g	H
Electrolytes	b		g	
Nutrients	A,b	A	g	
Enzymes	b		g	
Steroids	A,c,d	E	F	H

A = Barnett, How and Humphreys 1979a; b = Presidente and Correa 1981; c = Allen and Bradshaw 1980; d = Than and McDonald 1974a; E = Presidente *et al.* 1982; F = How *et al.* 1984; g = Presidente 1982b; H = Humphreys *et al.* 1984.