

Potential use of energy expenditure of individual birds to assess quality of their habitats

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ABSTRACT

Since animals show behavioural strategies that are sensitive to costs as well as gains, and because low or reduced energy expenditures are associated with longevity, it is argued that animals may generally seek to reduce living costs. Furthermore, as optimal foragers they may seek to minimise the ratio of costs to gains, so habitat selection should take account of living costs. This leads to the hypothesis that high-quality habitats will be generally cheap to live in. A number of factors could complicate this prediction by elevating costs independently of habitat: the form of the relationship between fitness costs and energy expenditure; breeding-status; indeterminate growth; distribution of individuals within habitat; genetic heterogeneity; predation risk; and pathogens. It is suggested nevertheless that free-living energy costs could provide important information regarding habitat quality where traditional methods are either inadequate or impractical.

Keywords: energy expenditure, fitness costs, habitat quality, habitat assessment.

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1. Introduction

Accelerated species extinction rates over the last few hundred years have led to concerns about how to maintain global biodiversity in the face of continued human development (Lawton & May 1995). Preservation of species is generally considered desirable for both practical and aesthetic concerns (Lawton 1997), and value is attached to habitats both as communities, and as environments essential to individual species. Since political processes will not conserve all remaining semi-natural habitats, it has often been the job of conservation managers to identify the most important of those remaining. At the community level, this is achieved through survey work to assess species diversity, or population sizes of scarce and rare species. Where a particular threatened species is targeted, the assessment of habitat quality has traditionally been conducted indirectly through measures of population density, breeding success, and survival (Van Horne 1983; Pulliam 1988). Habitats with more dense or more productive populations are assumed to offer the best chance for perpetuation of those populations in the future, and so are accorded a higher conservation status.

In areas of the globe where habitats are most threatened and where action is urgent, these methodologies are probably the most appropriate. However, where relict populations occur, survey techniques may identify where species persist, but fail to address the underlying causes of the current distribution (Wiens & Rotenberry 1981; Gray & Craig 1991; Clark & Shutler 1999). Stochastic events (anthropogenic or otherwise) may have caused present day distributions that have relatively little to tell us about species' requirements, and rather more to say about historical or ongoing factors. This is the more likely where population decline has been both recent and dramatic, as in New Zealand. In addition, the low dispersal rates of New Zealand's flightless birds, and of some volant birds with discontinuous habitat (Williams 1991), along with the generally low intrinsic reproductive rates of New Zealand birds, will tend to reduce the rate at which the most favourable habitats could be recolonised following local extinction. Accordingly there is a risk that surveys may fail to identify those habitats which offer the best long-term survival chances for populations.

In New Zealand, the pattern of human colonisation, along with introduced predators and habitat change, progressed from the coastal plains toward the mountains. Takahe *Porphyrio mantelli* were re-discovered in the remote Murchison Mountains, blue duck *Hymenolaimus malacorhynchos* inhabit upland rivers, much of the remaining habitat for forest birds is in upland areas that were either uneconomic to clear-fell, or not reached before conservation interests began to exert influence. Thus many native birds have current distributions that are essentially remote from humans. The conservation success story of predator-free lowland islands, however, has shown that upland habitat is not necessarily the most suitable for many species otherwise more or less confined to remote areas (Bell 1991).

Where populations persist, therefore, may simply be a matter of chance. Furthermore, favourable habitats may even have suffered a greater than random risk of species' extinctions: the most dense populations may have been targeted by introduced predators and hunters, and affected most by introduced parasites and other diseases. Channelling resources into conserving species in sub-optimal habitats is prodigal, but failing to identify the optimal habitat for endangered species could be fatal. To address properly the identification of habitat quality, a methodology that is independent of anthropogenic and historical factors is both desirable and potentially important.

The ensuing review seeks to assess whether measurement of daily energy expenditure (DEE) has the potential to identify favourable habitats within the current ranges of some endangered New Zealand bird species. It is assumed that DEE is a single measure of the interaction of physiological behaviour and the environment within individuals, and that low DEE implies good habitat quality.

2. Defining good habitat

2.1 USING DEMOGRAPHIC MEASURES

From the single-species conservation viewpoint, good habitat can be regarded as one with a higher than average chance of sustaining the target species into the future. Stochastic extinctions might tend to be more common in areas with higher productivity (for example, areas with rich fluvial soils are prone to catastrophic flooding), so the long-term fitness of animals that occupy such a site could be compromised. For animals confined to a few sites, or for those with poor dispersal, the 'best' habitat might not be that with the highest mean population size or productivity, but the one with the lowest variation in these measures. Hence, the appropriate time-scale over which to assess habitat quality might be millennia. The absence of long-term data sets prevents the identification of the most appropriate sites for conservation in such circumstances. More practical definitions have tended to revolve around the assumption that population density at carrying capacity can define habitat quality. However, density as an indicator of habitat quality (Van Horne 1983) should be used with caution, and should be accompanied by data on breeding success and survival where possible.

For animals in which dispersal between patches is significant, good habitat can be more easily identified, using the source-sink concept (Pulliam 1988, Dias 1996). Here a good habitat can be defined as that in which the average fitness of the population is greater than one, whilst poor habitat has a mean fitness of less than one (Diffendorfer 1998) and thus requires net immigration for its population to be sustained. However, as Watkinson & Sutherland (1995) have shown, sources and sinks, though conceptually uncomplicated, can be very problematic to identify in nature, even with a full knowledge of demographic rates. An energetic assay of habitat could not be expected to solve these difficulties, but, subject to rigorous testing, might provide a useful alternative

or additional means of identifying key populations and habitats for conservation.

2.2 WHY SHOULD GOOD HABITAT BE CHEAP TO LIVE IN?

Animals that are still capable of growth are not expected to minimise energy expenditure. This is because fecundity increases with body size (Stearns 1992), and hence for such animals good quality habitat is likely to be one in which individuals are larger. Since animals grow by increasing energy intake, energy expenditures are predicted to be higher in better quality habitats, simply because there is more food available (Karasov & Anderson 1984; Beaupre 1996). Animals that have already achieved their maximum potential size, however, can only store a limited reserve for future reproduction, and it is for such animals, in a non-growth phase that the arguments below have been developed. In volant animals particularly, the level of reserves is likely to be firmly constrained by the costs of carrying extra mass in flight, both physiological (Pennycuik 1989) and to do with predation risk (Gosler et al. 1995).

2.3 FITNESS COSTS OF ENERGY EXPENDITURE

The observation there is no such thing as a 'perfect organism' (one that is born breeding at the maximum possible rate, and that continues so to do throughout its infinite life span) is taken as evidence that energy is limiting reproduction (Williams 1966). Current interest in sustainable metabolic rates (SusMR) can be traced back to Drent & Daan's (1980) paper postulating a link between field metabolic rates (FMR) and basal metabolic rates (BMR). Drent & Daan (1980) suggested that the 'prudent parent' could not exceed an energy expenditure rate of 4 xBMR without incurring increases in mortality or fecundity costs. The possible role for central limits (digestion and absorption rates) as opposed to peripheral limits (rates of mechanical work, heat production and tissue growth) in determining SusMR has received wide interest in the physiological literature (Peterson et al. 1990; Weiner 1992; McDevitt & Speakman 1994; Konarzewski & Diamond 1994; Koteja 1996). Alternatively energy expenditure might be resource-limited (e.g. Juliano 1986).

It has been argued that, since energy is limiting, metabolic efficiency must be advantageous, because any energy saving can be diverted into reproduction (Norberg 1981). Furthermore, Priede (1977) has shown that selection for efficiency in locomotion could be very strong. However, seminal papers on the economic analysis of foraging decisions (MacArthur & Pianka 1966; Emlen 1966; Charnov 1976) disregarded foraging efficiency as a possible currency for optimal foragers. They reasoned that optimal foragers must always favour gain rate (gain/time) maximisation over efficiency (gain/cost) since the latter can lead to a reduction in overall energy gain, and hence a reduction in the energy available for reproduction. The concept of optimal resource allocation implies that maintenance costs should be minimised, but not that daily energy

expenditure should be. This is because energy should be spent in order to gather (or store) more resources for current (or future) reproduction.

Without a cost to energy expenditure itself, there seems to be no possible advantage to a strategy maximising foraging efficiency (Ydenberg et al. 1994). However, when the currencies of energy efficiency and gain rate maximisation have been specifically compared, the data from a variety of species have tended to lie closer to the predictions of the former (Schmid-Hempel et al. 1985; McLaughlin & Montgomerie 1985, 1990; Kacelnik et al. 1986; Tamm 1989; Welham & Ydenberg 1988, 1993; Ydenberg et al. 1994; Bryan et al. 1995; Welham & Beauchamp 1997). This finding implies that there is indeed a cost *per se* to energy expenditure. One study (Bryant 1991) has shown that birds with high energy expenditures in one breeding season are less likely to survive to breed again. Furthermore increased parental energy-expenditures consequent on clutch-size manipulations have been shown to reduce survival (Daan et al. 1996). In addition, there have been a number of experimental studies indicating a negative association between sexual activity (Partridge & Farquhar 1981) or foraging activity (Nur 1984; Schmid-Hempel & Wolf 1988; Wolf & Schmid-Hempel 1989) and life span.

2.4 RELATIONSHIP BETWEEN FITNESS COSTS AND ENERGY EXPENDITURE

The form of the relationship between fitness costs and energy expenditure has been variously considered (Sacher 1978; Drent & Daan 1980; Masman et al. 1989; Bryant, 1991, 1997; Bryant & Tatner 1991; Cartar 1992). There could be indirect fitness costs of energy expenditure if, for example, risk of predation increased with foraging activity (Lima & Dill 1990; Magnhagen 1991; Norrdahl & Korpimaki 1998). Alternatively costs could be more direct. Fitness could be compromised through 'wear and tear' at the cellular level (Sohal 1986; Ricklefs 1998). Temporary elevation of costs above a sustainable rate might compromise immune response (Konig & Schmid-Hempel 1995; Deerenberg et al. 1997), and render an animal more susceptible to disease. Alternatively the consumption of body reserves during negative energy balance could lead to an increased risk of starvation. It is these sorts of ideas that lie behind Drent & Daan's (1980) consideration of reproductive effort, and their conclusion that the fitness costs of energy expenditure rise steeply above a metabolic ceiling of 4 xBMR. Bryant & Tatner (1991), reviewing the available data on avian energy expenditure, found that, at least over short measurement periods (1-2 days), energy expenditures greater than 4 xBMR had been recorded in up to 30% of individuals and 48% of species. They argued that the balance of evidence suggested a more probabilistic and progressive increase in fitness costs with energy expenditure rather than a particular threshold. Furthermore Ricklefs (1998) has pointed out that average avian expenditures during breeding fall somewhat short of the proposed 4 xBMR ceiling. This suggests that birds usually maintain considerable spare capacity, and tends to support the contention that fitness costs exist below the proposed 'threshold'.

An alternative view of the relationship between fitness and DEE is the ‘rate of living’ theory (Sacher 1978; Sohal 1986; developed from Pearl 1928), which envisages a proportional relationship between energy expenditure and cell degeneration. Supportive evidence includes broad correlative support from comparative studies of metabolic rate and life-span (Calder 1984), but also experimental evidence showing that reduced energy expenditure is associated with longevity (Lyman et al. 1981). A similar argument to explain why bumble bees follow an efficiency currency was put forward by Cartar (1992), who found wing wear to be a proximate factor in their mortality rates.

3. Relationship between energy expenditure and habitat quality

A number of studies already provide some support for a relationship between habitat quality and energy expenditure (Hayes 1989; O’Halloran et al. 1990; Furness & Bryant 1996; Corp et al. 1997; Kilpi & Lindstrom 1997). Higher energy expenditures in poorer habitats can result directly from environmental effects on thermoregulatory costs (Kilpi & Lindstrom 1997), or may also include additional foraging costs to offset the energy lost through high-cost thermoregulation (Hayes 1989). Similarly Furness & Bryant (1996) have demonstrated that wind speed is an important determinant of field metabolic rates in the northern fulmar (*Fulmarus glacialis*), and have suggested that low wind speeds might limit the breeding range of Procellariiformes in general. Although they did not measure energy expenditure directly, Corp et al. (1997) have shown how food availability can affect high cost behaviours in rodents, with animals in habitat with low food availability hunting longer distances, over greater areas at faster average speeds. Time-energy budgets of dippers (*Cinclus cinclus*) occupying poor-quality (acidic) streams have been compared with those on high-quality (circum-neutral) streams (O’Halloran et al. 1990). Expenditure of male dippers tended to be higher in the poor-quality sites during the energetically cheapest season, but not during breeding. This study points to the importance of life-history stage in the relationship between habitat quality and energy expenditure, e.g. between breeding and non-breeding periods. However, this is but one of several issues which may complicate the general prediction of low living costs in good-quality habitats, as discussed below.

3.1 LIFE HISTORY STAGE

Recognising a fitness cost to energy expenditure, whether direct (through cell degeneration or reduced immune response) or indirect (through wear and tear or predation risk, associated with high-energy activities) (see above) has profound consequences for much ecological thought. Of interest in this context

is the relationship between foraging strategy and habitat selection. Optimal habitat selectors might once have been assumed to seek maximum gain rates, mirroring the gain rate maximisation currency of many model optimal foragers, and optimal breeders to work at the maximum possible rate, independent of habitat. However, in the light of fitness costs to energy expenditure, the debit as well as the credit must be considered. Animals are expected to maximise fitness by seeking to minimise the ratio of costs: gains (consistent with meeting certain minimum requirements for reproduction). A high-quality habitat can be viewed as one in which a given number of offspring can be reared for a lower level of effort, or where an equal energetic input could rear more offspring (e.g. Reyer & Westerterp 1985). Optimal parents should trade-off energy expenditure against offspring production, i.e. future against current reproduction (Williams 1966).

The outcome of this trade-off for a particular species could be predicted from its life history. Animals in good habitats, with low survival rates from one breeding period to the next, should tend toward higher investment in offspring, whereas those with high survival rates should tend towards lower energy expenditure. This is because the former may derive little benefit from a reduction in energy expenditure, since survival is in any case unlikely, whereas the latter should not compromise survival to the next breeding season (Bryant 1991, Lemon 1993; Daan et al. 1996; Kersten 1996) because they have more reproductive potential to lose.

A rather more straightforward prediction can be generated for the DEE of non-breeding individuals: identical animals should have lower living costs in good habitats than in bad. This is because the resources necessary for survival are available at lower cost (i.e. a lower cost: gain ratio). In addition, since their access to exogenous resources is more assured, animals in high quality habitats should require fewer endogenous reserves, and thus incur lower maintenance metabolism (Witter & Cuthill 1993).

3.2 FORM OF THE RELATIONSHIP BETWEEN FITNESS COSTS AND ENERGY EXPENDITURE

General predictions regarding the relationship between energy expenditure and habitat quality are made complicated, because the form, or forms, of the relationship between fitness costs and energy expenditure is not known. If either the 'cost of living' theory, or if Bryant & Tatner's (1991) idea of a progressive increase in fitness costs with DEE is correct, then the above predictions hold. However, if Drent & Daan's (1980) notion of a steep increase in costs at a given multiple of BMR is closer to the truth, the fitness costs of energy expenditure are, essentially, either on or off. During the breeding season we expect animals in all habitats to approach close to the energy expenditure at the inflection of the curve, but not exceed it. The rapidly accelerating costs of doing so would be likely to outweigh any incremental benefits in offspring fitness. Similarly, parents would receive a trivial increase in fitness from any reduction of DEE below the inflection compared to the reduction in offspring fitness. As a consequence no difference in energy expenditure would be predicted between good and bad habitats during the breeding season.

Similarly, if fitness costs are essentially equal over the lower range of energy expenditures during the non-breeding season, animals in high-quality habitats may be expected to have expenditures indistinguishable from those in poorer habitats. In this case, habitat quality could be distinguished using time budgets. For example, non-maintenance activities would be expected to constitute a larger part of the daily schedule of an animal in a good habitat, since 'spare' energy is more readily available there. Without accompanying energy budgets, this behavioural information would be less useful, since the importance of non-maintenance activity is difficult to unravel.

3.3 DISTRIBUTION OF RESOURCES AMONGST INDIVIDUALS

Models of habitat use and dispersal (Fretwell & Lucas 1970; Pulliam 1988; McPeck & Holt 1992; Diffendorfer 1997) have highlighted the importance of dispersal in determining habitat quality for the individual. The ideal free distribution (Fretwell & Lucas 1970) suggests that dispersal can equalise individual fitness across heterogeneous sites. Despotic territorial behaviour can maintain a population distribution in which superior competitors exclude intraspecifics from preferred habitat, and achieve higher reproductive success (e.g. Møller 1995).

Where an ideal free distribution exists, energy expenditures as well as fitness might be expected to be equal amongst habitats, with 'quality' discernible only through breeding density. Net gain rates could be equalised amongst patches with population density tracking differences in resource densities. However, where despotic territoriality exists, maintenance costs should vary negatively with resource density. This is because, even if all territories across habitat types contain an equal amount of resources, locomotion costs associated with territory exploitation will tend to be negatively correlated with resource density. Johnstone (1994), for example, has shown a positive correlation between territory size and free-living energy expenditure in a population of non-breeding European robins *Erithacus rubecula*. It is possible that low maintenance costs associated with small territories might be offset by (positive) density-dependent territorial costs, but on the other hand, large territories could be more costly to defend (Kodric-Brown & Brown 1978).

Thus we expect to find a relationship between habitat and energy expenditure more reliably amongst despotic territorial animals, or where population density is so low that suitable habitat remains unoccupied.

3.4 GENETIC HETEROGENEITY

Where populations exhibit significant genetic differences, the suggested habitat-energy interaction could be complicated by local selection. These might be expected to tend to equalise expenditure across habitat types, given that the fitness costs associated with energy expenditure are likely to be systematic, or at least general.

Similarly, on a local scale, individuals of high competitive ability could potentially have heritable differences in metabolism. The association between BMR and FMR (Drent & Daan 1980; Daan et al. 1991; Walton 1993; Ricklefs et al. 1996) is likely to mean that dominant animals tend to have higher field metabolic rates, if, as demonstrated by Bryant & Newton (1994) they have higher basal metabolism. The association between dominance and high FMRs has been experimentally demonstrated in lizards, by manipulating testosterone levels (Marler et al. 1995). Such a relationship would tend to mask a negative correlation between habitat quality and energy expenditure, since high-cost dominant individuals should occupy (putative) low-cost high quality habitat, forcing sub-dominants into more expensive habitats. Once again the potentially confounding variable should increase the chances of accepting a false null hypothesis when seeking a negative relationship between FMR and habitat quality, and increase confidence in its reality if such a relationship were found.

3.5 PREDATION RISK

Numerous studies have demonstrated that animals trade-off predation risk against energy intake (reviewed by Lima & Dill 1990), and an energetic equivalence of predation risk has been claimed to be determined (Abrahams & Dill 1989, Pettersson & Bronmark 1993). Furthermore, the reserves carried by both birds and mammals have been shown to be highly sensitive to predation pressure, although not always in a consistent manner (e.g. Gosler et al. 1995, Lilliendahl 1998). Nevertheless, the role of predators in influencing the energy expenditure of their prey has received no direct attention in the literature. Yet its importance is likely to be widespread, and predation may have played a crucial part in the evolution of energy metabolism.

The presence of predators in a habitat could have both direct and indirect effects on the energy expenditure of potential prey. Direct effects are those resulting from behavioural responses to predation risk, whereas indirect effects might flow from predator influences on prey population density, and on resource density. In both cases predation pressure could work either to increase or decrease energy expenditure.

Direct effects likely to reduce expenditure would include an increase in prey vigilance behaviour (low cost) at the expense of foraging behaviour (high cost). Furthermore predators might tend to suppress expensive non-maintenance behaviours in their prey, such as sexual or territorial display. The presence of predators is generally thought to cause an adaptive reduction in mass amongst prey species (McNamara & Houston 1993; Gosler et al. 1995). This would tend to reduce daily energy expenditure (DEE) per bird, even though costs per gram of tissue might increase, since a high proportion of mass loss consequent on predator presence would be expected to be in the form of lipid reserves (of low metabolic activity). Nevertheless, any reduction of mass should lead to an overall reduction of maintenance and locomotion costs. In addition, the reduction of DEE could result from the indirect effects of predators on prey population density. Any impact of predators on prey population density could be expected to lead to an increase in food availability and a reduction in intra-specific contests.

On the other hand predators might increase the living costs of their potential prey by promoting higher levels of awareness, and discouraging night-time hypothermia (an adaptive energy-saving tactic in some birds). Birds might be induced to make more short, 'nervous' flights where their risk of predation is high, and active fleeing from predators could also increase living costs relative to predator-free habitats. Predators might indirectly increase prey living costs by leading to an increase in prey territory size following population reduction. Larger territories might have higher costs, both in terms of defence and exploitation (Kodric-Brown & Brown 1978; Johnstone 1994). If the predators are omnivorous, they might reduce prey resource-density, in which case their presence could tend to increase prey DEE by elevating resource acquisition costs.

In any event, predators are likely to have important consequences for prey energy-expenditures, which could be independent of habitat quality.

3.6 PARASITES AND PATHOGENS

The risk of infection or its actuality may be expected to affect DEE. On the one hand the advantages of reducing possible contact with infection might impose lower activity levels, whilst on the other, actual infection could either increase living costs following increased energy investment in immune defence (Møller et al. 1998), or reduce them if vitality is compromised.

There is evidence that anti-parasite investment is condition dependent (Saino & Møller 1996; Møller et al. 1998). This being so, the occupants of high-quality habitat could exhibit higher living costs than those from poorer habitats with fewer 'spare' reserves. In addition the probable positive association between pathogen and host population density could mean that a higher level of investment in immune defence would be more advantageous in populous, high-quality habitat.

It is apparent that disease might obfuscate any underlying relationship between energy expenditure and habitat quality. Furthermore, it is likely that case-specific effects could serve either to reduce or increase DEE independently of habitat quality.

4. Conclusions

There are good reasons for expecting individuals living in high-quality habitat to have low maintenance expenditures. These derive from a presumed fitness cost attached to energy metabolism, for which evidence is widespread. The form of this fitness cost may have consequences for the generality of an effect of habitat quality on energy expenditure. As argued above, such a relationship is more likely to apply to certain types of organisms and life-history stages than others. Territorial individuals during a non-growth, non-breeding period are likely to display the relationship most clearly. While there are a number of potentially

confounding factors, these, with the exception of the effects of predation and pathogens, are likely to make the relationship between habitat quality and energy expenditure harder to detect rather than to alter it fundamentally. Thus, measurement of free-living energy expenditure of individuals may provide a rapid preliminary assessment of relative habitat quality sufficient to help focus further studies or assist conservation management planning. Studies which specifically compare DEE of individuals living in diverse habitats which, by other measures, are considered to be of differing qualities would help to test further the utility of DEE as a measure of habitat quality

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