

Energy expenditures of North Island robins in habitats with differing predator densities

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ABSTRACT

An investigation into the effects of introduced predators on the energetics of North Island robin, *Petroica australis longipes*, suggested that predation pressure could constrain energy expenditure by imposing a reduction in time devoted to energetically costly behaviours, such as foraging activity. Any energetics-based approach to habitat assessment should be accompanied by time budgets of the individuals involved.

Keywords: energy expenditure, habitat assessment, predator impact, North Island robin, *Petroica australis longipes*.

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1. Introduction

Introduced mammalian predators have been identified as one of the main influences contributing to the decline and extinction of New Zealand's endemic birds (Bell 1991). So pervasive and continuing are the effects of mustelids, rodents and possum that 'control' of these predators is attempted annually over vast areas of New Zealand forests, by means of aerial distribution of 1080 or brodifacoum poison baits.

There is a widespread belief that a reduction in rodent and possum densities 'improves' forests as habitats for insectivorous and folivorous birds (M. Williams, pers. comm.). While there is abundant evidence that a reduction in predation pressure *per se* improves breeding success and increases annual survival of many bird species, e.g. for kokako *Callaeas cinerea* (Innes et al. 1999), seemingly there have been no studies that have attempted to tease out the separate contributions that invertebrate population recovery and/or vegetation recovery may make to any 'improvement' in forest bird habitat quality. Given the long life cycles of many forest invertebrates and the slow and seasonally dependent responses of plants to release from browsing pressure, the most immediate and noticeable change in forest habitat 'quality' following aerial poisoning operations is undoubtedly the reduction (or elimination) of predation. Therefore, any comparison of energy expenditures of forest birds, e.g. North Island robins *Petroica australis longipes*, in two forest patches with different but recent histories of poison bait application is primarily a comparison of the influence of differing predator densities rather than of more widespread differences in resources available to the birds.

In the study described below, an attempt was made to test the hypothesis that in a forest habitat with low predator density, daily energy expenditure of North Island robins is lower than for robins living in similar habitat but in the presence of a greater density of predators.

2. Methods

A total of 40 NI robins from two areas of Pureora Forest Park, North Island, New Zealand, were caught using either mist-nets or clap-traps between January and April 1998. Birds were weighed (± 0.1 g) using a Pesola 50 g balance, and unbanded birds were marked using a unique combination of metal and colour bands. Tarsus, length of head + bill, keel length, and bill depth were measured using calipers accurate to ± 0.1 mm. Fat scores both tracheal and sternal (scale 0-5) were estimated, and a visual estimate of the bulk of the pectoral muscles was made (scale 0-5) (Gosler et al. 1995).

2.1 SITES

Plots at Tahae and Waimanoa were treated with an aerial drop of 1080 poison in August/September of 1996 and 1997, respectively. This treatment resulted in an immediate and comprehensive reduction in numbers of introduced mammals (rats, mice, stoats and possums) as estimated from transect sampling at each site (R.G. Powlesland unpubl. data), which returned to background levels in two or three years. Studies at these and other sites in Pureora Forest have shown a marked concomitant effect on robin breeding success (R.G. Powlesland unpubl. data), which is inferred to be due to a reduction of predation pressure. These suggest 70–80% of broods are successfully raised in the first breeding season after a poison drop, 30–40% in the second breeding season, and 10–20% in subsequent seasons, or where no poison had been deployed (R.G. Powlesland pers. comm.). In addition, robin population density at breeding time is probably highest in the second season after a poison drop, as local recruitment from the previous (most successful) breeding season exceeds local mortality.

To investigate the effects of predator density, robins were sampled at Waimanoa (low predator numbers) and Tahae (intermediate predator numbers). Where there were high numbers of predators, robins were too scarce to obtain any samples.

2.2 DOUBLY LABELLED WATER TECHNIQUE

The doubly labelled water (DLW) technique (Lifson & McClintock 1966; Tatner & Bryant 1988) involves capture of the focal animal, injection of stable (i.e. non-radioactive) isotopes of hydrogen (^2H) and oxygen (^{18}O) in the form of water, and a period of restraint allowing equilibration of the isotopes in the body water pool before a sample of the initial isotopic enrichment levels of the body water is taken. This is normally taken in the form of blood (c. 0.1 mL). Subsequently the animal is released into the wild for a period before a second capture is made. This period should be a multiple of 24 hours, since most animals structure their lives (and hence energy expenditure patterns) on a daily basis. The number of days depends on the metabolic rate and size of the animal, and, to a lesser extent, on the initial isotopic enrichment level. On recapture, a second ('final') sample of the body water is taken. The energy expenditure can then be calculated using the principles of indirect calorimetry (Brody 1945) from the depletion rate of the isotopes in the body water between the initial and final samples. Isotope abundance in samples is calculated as a proportion of total oxygen/hydrogen, measured using mass spectrometry. Full details of these procedures can be found in Tatner & Bryant (1988).

2.3 DLW FIELD PROTOCOL

Immediately after capture, robins were weighed and injected with DLW at 10 $\mu\text{L/g}$ body mass. Injection was intra-peritoneal, and the injectate was made up from 20.0 APE H_2^{18}O and 99.8 APE $^2\text{H}_2\text{O}$. After a period of 60 minutes equilibration, during which robins were restrained in bird-bags, a blood sample

of c. $10 \times 5 \mu\text{L}$ capillary tubes was taken, either from the femoral vein, or the brachial vein, using sterile needles for venipuncture. The site was cleaned with alcohol prior to puncture, and subsequently treated with antiseptic. The capillary tubes were flame-sealed immediately on collection. Birds were held for a further two minutes following blood sampling before being released, to insure that the wound had healed.

Birds were re-caught approximately 48 hours after initial release, and, after weighing, a second blood sample was taken in the same manner as above, using the opposite of the paired femoral/brachial veins.

2.4 ENVIRONMENTAL VARIABLES

Maximum and minimum shade temperature in the bush (at c. 1 m above ground level) was recorded daily at both sites ($\pm 0.1^\circ\text{C}$). Over the 48 hour period this yielded two maximum and two minimum temperatures.

2.5 TIME BUDGETS

An attempt to obtain time budgets of non-breeding robins proved unsuccessful, since robin behaviour was markedly affected by observer presence. Maintenance of adequate distances from focal birds to avoid this effect, whilst simultaneously monitoring their activity, was rarely possible.

2.6 STUFFED PREDATOR EXPERIMENT

Nest site

When differences in energy expenditure between sites were detected, and because no time budget data were available from which to seek explanations, an experiment was designed to test for possible effects of predators and robin population density on robin behaviour. In December 1998, at seven nest sites in the Waipapa Ecological Area and Waimanoa (all during the chick-rearing stage), a series of presentations were made at daily intervals (± 0.5 h). These comprised a stuffed stoat (STOAT), a toy rabbit (CONTROL) of similar size to the stoat, and a stuffed female robin (SR). Order of presentation at each nest was randomised, and each of the three objects was positioned as close as possible to, but not closer than, 3 m from the nest. Some nests were more difficult to access than others, and for the highest ones, object distance was as much as 8 m from the nest. However, at each nest site, the three objects were positioned at exactly the same spot. Thus the distance from presented object to nest differed between nests, but not between objects. The nest site was observed for one hour after the positioning of the object. In addition to time budgets of the male and female around their nest-site area, the numbers of nest visits and instances of chick-feeding were recorded for each of the three treatments. Time budgets distinguished the following mutually exclusive behaviours: perching; flying; hopping; preening; brooding; feeding chicks; and singing. The number of

individual flights made was also noted. In addition, distinction was made between time spent above 2 m in canopy; time spent below 2 m in the canopy; and time spent on the ground.

Feeding

To investigate further possible effects of predators on foraging activity in robins, the stuffed stoat and the toy were presented to robins while they were feeding on mealworms. Robins at these sites have been trained to feed on mealworms thrown on to the forest floor, and most did so freely and tamely, being attracted by the sound of tapping the mealworm container. For individual birds, both STOAT and CONTROL were presented sequentially (in randomised order) by placing them on the forest floor, attracting the robin to the site, and throwing mealworms at 15 s intervals (up to a maximum of 10 worms), as close as possible to the presented object. The number of flights made, the number of mealworms taken, and the time spent at differing heights in the canopy during the feeding session was recorded for each treatment.

3. Results

3.1 BLOOD SAMPLING

Attempts to extract blood from the femoral vein did not prove successful, due to difficulty in obtaining a sufficient volume of blood. Consequently the brachial vein was adopted as the site for venipuncture. Although sometimes regarded as a less suitable site because of the risk of getting blood on feathers, thus disrupting their insulatory function and increasing thermoregulatory costs, the brachial vein proved ideal. Wounds healed quickly, and a controlled flow of blood, such that none spilled on to feathers, was usually possible.

3.2 BEHAVIOUR

On release, birds flew instantly, usually to a perch about 5 m from the release site, where they preened briefly (c. 5 s) before flying out of sight. No unusual behaviour was observed during the DLW period, but all robins became considerably less tame than formerly. Most birds, particularly juveniles, regained their former tameness over a short period of time. A few birds apparently 'disappeared', although they could be heard singing on their territories in the normal way, and only became tame again over a period of weeks. Only the (initially) tamest birds were re-caught. The effect on tameness was similar to, though probably more pronounced than, the effect caused by capture and banding alone (R.G. Powlesland pers. comm.).

3.3 RECAPTURE

Only 11 (28%) of birds were recaptured within the 48 hour time window. Six of these were from Tahae and five from Waimanoa; these comprised seven males and four females, or three adults and eight independent young of the year.

3.4 ENERGETICS

Details of individual robins are given in Table 1. Mean mass at recapture 29.49 ± 0.52 g) did not differ significantly from the mean mass at initial release 29.55 ± 0.56 g) (paired *t*-test, $t_{11} = 0.07$, $P > 0.9$), indicating that birds did not lose mass following the DLW treatment.

A simple comparison of birds at Tahae (high predator numbers) and Waimanoa (low predator numbers) revealed no significant difference between the average daily metabolic rate (ADMR) ($\text{mL}^3 \text{CO}_2/\text{g}/\text{h}$) of the two populations (mean \pm SD T: 3.89 ± 0.41 ; W: 4.27 ± 0.25 ; $P < 0.31$). When mean maximum temperature and mean minimum temperature were entered as covariates in a general linear model (GLM), however, the ADMR of robins at Waimanoa was significantly higher than at Tahae (adjusted least squares means \pm SD Tahae: 3.49 ± 0.19 ; Waimanoa: 4.75 ± 0.21 ; $P < 0.008$). Using either daily energy expenditure (DEE, kJ/bird) or energy expenditure expressed as a multiple of metabolic rate ($\times \text{BMR}_{\text{A\&P}}$, calculated from the Aschoff & Pohl (1970) standard equation for passerine birds), this pattern remained significant, though at lower probability levels ($P < 0.02$ and < 0.05 , respectively). Using a single overall temperature measure (the mean of maximum and minimum temperatures), the site effect on ADMR was no longer significant ($P < 0.117$) suggesting that minimum and maximum temperatures had independent effects on energy expenditure.

TABLE 1. DETAILS OF INDIVIDUAL NORTH ISLAND ROBINS AND THEIR ENERGY EXPENDITURES.

INDIVIDUAL	SITE	SEX	AGE	STAGE	MASS	ADMR* (kJ/day)	DEE	$\times \text{BMR}_{\text{A\&P}}^\dagger$
Graham	Waimanoa	male	adult	breeding	27.9	4.89	86.61	2.43
Enid	Tahae	female	adult	breeding	26.9	4.62	78.94	2.27
Gotz	Tahae	male	yoy [‡]	yoy	31.0	4.57	89.95	2.34
Zoro	Tahae	male	yoy	yoy	32.8	3.49	72.58	1.81
Jenny	Waimanoa	female	yoy	yoy	29.0	4.23	77.86	2.12
Josef K	Waimanoa	male	yoy	yoy	31.7	4.57	91.96	2.35
Jason	Waimanoa	male	adult	moult	30.4	4.11	79.32	2.09
Raul's juv	Waimanoa	female	yoy	yoy	29.6	3.55	66.74	1.79
Feshie	Tahae	male	yoy	yoy	30.4	3.75	72.31	1.90
Vamp	Tahae	female	yoy	yoy	28.3	2.97	53.28	1.48
Prufrock	Tahae	male	yoy	yoy	30.5	3.94	76.21	2.00

* ADMR, average daily metabolic rate ($\text{cm}^3 \text{CO}_2/\text{g}/\text{h}$).

† $\times \text{BMR}_{\text{A\&P}}$, multiple of basal metabolic rate predicted by Aschoff & Pohl's (1970) equation for passerine birds.

‡ yoy, young of the year.

Considered as a multiple of basal metabolic rate, the energy expenditure of NI robins across sites was 2.05 (\pm 0.29). This is rather lower than is typically recorded for passerines (Bryant 1991; Bryant & Tatner 1991).

DEE was not significantly correlated with any of the measures of structural size, nor with fat score, nor with mass. There was a significant positive correlation between DEE and bulk score (see Methods) ($P < 0.03$), but after application of the Bonferoni correction for multiple tests, this did not remain significant.

3.5 STUFFED PREDATOR EXPERIMENT

Nest site

Nest visits by adults to feed chicks were significantly less frequent in the presence of the STOAT than with either the CONTROL or the stuffed robin (SR) ($F_{2,20} = 3.83$, $P < 0.04$), with Scheffe contrasts revealing no significant difference between nest visits for CONTROL or SR treatments, but that STOAT treatment depressed feeding visits with respect to both SR and CONTROL. An ANOVA for total visits was marginally non-significant ($F_{2,20} = 3.15$, $P < 0.07$), but showed the same trend. A paired sample *t*-test, accounting for between-nest variation, demonstrated that STOAT caused a highly significant reduction in both total nest visits and chick-feeding visits with respect to the CONTROL ($t_6 = 3.71$, $P < 0.009$ and $t_6 = 4.51$, $P < 0.005$, respectively).

Overall, the time budgets of male robins were similar between treatments. The proportion of time spent at differing heights in the canopy was highly variable between individuals, but not between treatments. Of the mutually exclusive behaviours, only the amount of time spent flying differed between treatments, with ANOVA indicating a weak trend ($F_{2,15} = 3.83$, $P < 0.046$) for reduced flying time in the STOAT treatment with respect to the CONTROL and the SR treatments. This tendency for flight reduction in the presence of the stuffed stoat was more marked in the number of individual flights made ($F_{2,15} = 5.52$, $P < 0.016$).

Feeding

In the feeding experiment, the presence of the stuffed stoat led to a decrease by around 50% in the rate of mealworms taken by robins with respect to the control (mean mealworms taken per min \pm SD: STOAT 2.29 \pm 1.24; CONTROL 3.30 \pm 0.41; paired $t_{16} = 3.25$, $P < 0.005$). As a consequence, robins took fewer mealworms when the STOAT was presented, although this did not differ significantly from the CONTROL group ($P < 0.22$). The number of trivial flights made by robins during the experiments differed significantly between groups, with fewer made in the presence of the STOAT (mean flights/min \pm SD: STOAT 2.16 \pm 0.90; CONTROL 3.38 \pm 1.98, paired $t_{16} = 2.37$, $P < 0.031$). In addition, the presence of the stuffed stoat caused robins to modify their habitat use, tending to reduce the amount of time spent on the ground and increase the time spent higher in the canopy.

4. Discussion

In the absence of replication, conclusions regarding the source of differing energy expenditures of robins between the two sites can only be made tentatively. Firstly, the between-site difference in ADMR might result from factors other than predator numbers. Gross habitat structure could cause differences in energy metabolism; however, each site appeared to have considerable heterogeneity of vegetation and topographical structure, such that within-site variation was greater than between-site variation. Although the two sites were sufficiently close to each other (c. 15 km) for a general difference in weather pattern to be unlikely, their differing altitude might have caused varying expenditures between sites. However, as both minimum and maximum temperatures were accounted for in the GLM, this most obvious source of a climatic effect can be ruled out.

If predator numbers were ultimately responsible for the different energy expenditures between sites, these may have followed from either direct effects on behaviour, or indirect effects on habitat and neighbourhood structure. Robin population density could have important effects on behaviour, e.g. robins in a high density population spent more time foraging than those in a population with larger territories (Powlesland 1981). Although direct measurements were not available here, there was no obvious difference in population density between the two sites.

The results of the stuffed predator experiment suggest that in any case the impact of other robins might be low compared to that of predators. No differences were detectable between the behaviour of the nesting pair when presented with CONTROL or SR objects, whereas the STOAT treatment resulted in many differences from the other two. Nor was it the case that the stuffed robin was instantly and easily recognised as a fake by the incumbent birds. Six of the seven incumbent pairs appeared to recognise the stuffed bird as a genuine intruder, whilst two of the pairs made repeated, though short-lived, attempts to dislodge the stuffed bird throughout the 1-hour observation period. One of these two pairs also made repeated attempts to dislodge the stuffed stoat. Although incumbent birds clearly perceived an intruder on their territory, their resultant behavioural schedules were not markedly different from that in the CONTROL treatment, and would not lead to an expectation of a significant change in energy budget. It should be stressed that the presentation of a stationary robin near a nest site only mimics the impact of population density on intra-specific interactions, and this experiment has no bearing on resource density aspects of population density.

In the same way, the presentation of a stuffed stoat did not exactly reproduce the experience of birds living under a regime of higher predator density. Nevertheless, robins responded to the predator as if it were real, and that response resulted in behaviour likely to be of lower metabolic intensity; birds of both sexes made fewer visits to the nest, and fed the chicks less in the STOAT treatment. Males spent less time flying, and made fewer individual flights. Similarly, in the feeding experiment birds made fewer flights/min, and took fewer food items/min in the presence of the stuffed stoat, and even modified

their structural habitat use. Flight is regarded as the most energetically expensive behaviour in a bird's repertoire, and the cost of short ('trivial') flights in European robins (*Erithacus rubecula*) has been indirectly measured as 23 xBMR (Tatner & Bryant 1988).

These points suggest that predators could force down living costs of robins, by reducing both foraging costs and food intake. If this were generally the case, robins at Tahae might be expected to be in poorer condition than Waimanoa birds. However, there was no difference between mean mass at Tahae (29.81 ± 2.64 g, $n = 22$) and Waimanoa (29.75 ± 1.67 g, $n = 18$) ($t_{38} = 0.09$, $P > 0.92$), nor did a significant difference emerge when controlling for structural size differences. The reduction in energy expenditure at Tahae is presumed to be matched by the reduction in energy intake. Surprisingly, this implies that predators do not impose a fitness cost on free-living robins but modify their habitat exploitation. This may indeed be the case if adult birds are not at significant risk of predation whilst foraging and robins suffer predation only as eggs, chicks, or roosting/incubating adults. As the results of the nest-site stuffed predator experiment suggest, breeding robins are most likely to reduce energy expenditure in the presence of predators, and chick growth rate could be similarly affected. Several pairs made no visits to their nest at all while the stoat was in place, but instead inspected it from a distance, with a beakful of uneaten invertebrates. Clearly robins are likely to maximise fitness by temporarily reducing energy delivery to the nest to avoid leading a predator to its chicks. Where nest predation is significant and predator density high, energy expenditure of breeding birds may be *positively* correlated with habitat quality, as seems to be the case here.

The energetic measurements point towards an effect of predation in reducing living costs of robins, which receives support from both the feeding experiment and the nest-site experiment involving stuffed predators. This interpretation consolidates a growing understanding regarding the role of foraging in mediating the trade-off between mortality and growth (Lima & Dill 1990; Magnhagen 1991; Werner & Anholt 1993; Norrdahl & Korpimäki 1998) by introducing an energetics component. This allows an analysis of the effect of day-to-day foraging decisions on physiology, and ultimately, fitness.

The results presented here illustrate that the DLW method is sensitive enough to detect differences in energy metabolism between birds in different semi-natural habitats, and point towards the utility of the technique for habitat assessment. However, this investigation of the way in which predation risk might alter the general prediction that good habitat should be cheap to live in has underlined the need to understand the proximate causes of differing energy use. It would be naïve to expect good habitat and cheap living costs to be inextricably linked, since reducing energy costs is only one component of fitness. The risk of being eaten is another, and where this risk has been manipulated we should expect to find a significant impact. The most appropriate application of the low-cost high-quality habitat principle is likely to be a situation where resource density or quality determines energy flow. Since the assumption that this is always the case cannot be reliably made, some attempt to record the behaviour of individuals is essential if DEE is to be linked to habitat quality. Some aspects of energy metabolism may be fixed, but others fall within the decision-making environment of animals. Like all choices that

animals make, those affecting energy expenditure must be traded off against others if fitness is to be maximised.

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6. References

- Aschoff, J.; Pohl, M. 1970: Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *Journal of Ornithology* 111: 38–47.
- Bell, B.D. 1991: Recent avifaunal changes and the history of ornithology in New Zealand. *Acta XX Congressus Internationalis Ornithologici*: 195–230.
- Brody, S. 1945: Bioenergetics and growth: with special reference to the efficiency complex in domestic animals. Hafner, New York.
- Bryant, D.M. 1991: Constraints on energy expenditure by birds. *Acta XX Congressus Internationalis Ornithologici*: 1989–2001.
- Bryant, D.M.; Tatner, P. 1991: Intraspecific variation in avian energy expenditure: correlates and constraints. *Ibis* 133: 236–245.
- Gosler, A.G.; Greenwood, J.J.D.; Perrins, C. 1995: Predation risk and the cost of being fat. *Nature* 377: 621–623.
- Innes, J.; Hay, R.; Flux, I.; Bradfield, P.; Speed, H.; Jansen, P. 1999: Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation* 87: 201–214.
- Kacelnik, A. 1979: The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Animal Behaviour* 27: 237–241.
- Lifson, N.; McClintock, R. 1966: Theory and use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* 12: 46–74.
- Lima, S.L.; Dill, L.M. 1990: Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- Magnhagen, C. 1991: Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* 6: 183–186.
- Norrdahl, K.; Korpimäki, E. 1998: Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology* 79: 226–232.
- Powlesland, R.G. 1981: Comparison of time-budgets for mainland and Outer Chetwode Island populations of adult male South Island robins. *New Zealand Journal of Ecology* 4: 98–105.
- Tatner, P.; Bryant, D.M. 1988: Doubly-labelled water technique for measuring energy expenditure. Pp. 77–112 in: Bridges, C.R.; Butler, P.J. (eds) *Techniques in comparative respiratory physiology: An experimental approach*. Cambridge University Press, Cambridge.
- Werner, E.E.; Anholt, B.R. 1993: Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142: 242–272