Effect of radio transmitters on energy expenditure of takahe

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ABSTRACT

The energy costs to takahe, *Porphyrio mantelli*, of bearing radio transmitters was investigated for tagged and untagged control birds using the doubly-labelled water technique. Using repeated measures sampling of six individual takahe at Burwood Bush Research Station, Te Anau, New Zealand, the mean daily energy expenditure (DEE) of birds carrying backpack radio-transmitter packages (mass 48.1 g equal to 1.39–2.28% body mass) was 1269 kJ. This compared with control birds with daily expenditures of 1179 kJ. The difference was significant at $P < 0.05$ and amounted to a 7.7% increase in free-living costs for tagged individuals. Using general linear modelling to control variation from other sources, the increase in DEE due to tags was estimated at 8.6%. Time budgets indicated no significant impact of tag-bearing on behaviour, and although statistical power was low, these data suggest that behavioural differences were unlikely to account for the observed differences in energy expenditure between groups. Mechanical power required for muscular support of the extra mass did not explain more than 15% of the observed increase in living costs. We suggest that the principal cost of tag-bearing is derived from increased thermoregulatory costs consequent on feather disruption by the tag and/or harness. As the scale of increase in expenditure due to tags might be sufficient to compromise survival and/or reproductive success, we suggest that improvement of tag-design should be considered.

Keywords: energy expenditure, radio transmitters, takahe, *Porphyrio mantelli*, thermoregulation.

1. Introduction

Radio-location technology has become widely available, and radio- or acoustic-telemetry is now routinely used in the investigation of animal ecology and behaviour. It is an underlying assumption of such studies than bearing radio-transmitters does not significantly alter behaviour, and that tagged animals remain representative of the wider population. Yet this assumption is not usually tested (White & Garrott 1990).

Whilst technological advances enable the tele-collection of sophisticated data sets, and a reduction in transmitter mass, the overriding factor controlling the mass of the entire tag-package (hereafter termed tag) is usually the battery. Researchers must balance the benefits of long-lived batteries for data collection against the effect of heavier tags on their carriers (Kenward 1987; Hill et al. 1999). A maximum body mass: tag mass ratio of 20:1 has been suggested (Cochran 1980: Kenward 1987; White & Garrot 1990), but this figure is some-what arbitrary, and ignores size-dependent strength:mass ratios. Theoretical calculations (Caccamise & Hedin 1985; Marden 1987) of surplus power in flighted birds imply that smaller species should be capable of carrying proportionally greater loads than larger birds. Similarly, different modes or media of locomotion may be associated with differential tag mass-dependent effects, due to different mechanics (Roberts et al. 1998) and differential drag effects (Orbrecht et al. 1988; Bannasch et al. 1994). No guidelines covering these issues are available to those planning radio-tracking studies.

The method of attachment of the transmitter to the animal is a second area of concern. Radios have been glued, tied, sutured, clamped, harnessed, anchored, implanted, and even attached by suction to various animals. Each method has its critics and defenders, and various controlled experiments have shown one or other method to be preferable for particular reasons on particular species. However, few, if any, authors have felt inclined to extend their individual findings to a recommendation for a particular attachment method for wider ecological or taxonomic groups.

With no clear evidence to influence the choice of transmitter mass or attachment method for particular animals, researchers must endeavour to ensure that tags do not significantly affect the welfare, behaviour, and fitness of their study species. Behavioural effects of tags can be more readily assessed than effects on reproductive success and survival, and have been widely examined. However, the evidence that behavioural studies can yield is somewhat limited, since physiological costs of tag-bearing may not be expressed behaviourally, and studies must inevitably concentrate on particular aspects of behaviour, whilst overlooking others.

Consequently, absence of evidence of behavioural effects cannot be reliably taken as evidence of absence of an effect of tag-bearing, though, in fact, this is often an implicit assumption of such work (e.g. Neudorf & Pitcher 1997).

Evaluating effects of tags on survival and reproductive success can provide much less equivocal evidence, although this approach presents other problems:

- effects on long-lived organisms may take place on a time-scale beyond the duration of the study;
- comparable data for untagged and tagged individuals may be difficult to obtain;
- large sample sizes may be required to achieve adequate statistical power for estimates of survival and reproductive success;
- the risk of increased mortality might jeopardise approval for the effects of tags to be tested over the long term in rare animals.

Here we demonstrate that daily energy expenditure (DEE) can be used to examine potential costs of tag-bearing, and we apply the doubly labelled water (DLW) technique (Tatner & Bryant 1988) to measure these costs in an endangered flightless bird species, the takahe, *Porphyrio mantelli*. DEE is a measure of the outcome of the interaction between behaviour and physiology. It can therefore provide evidence regarding potential long-term effects of tag-bearing without imposing a long period of possible hardship on an animal. This approach is not novel, but has received little attention, and studies to date have mostly had small sample sizes (Nagy et al. 1984, Gessaman & Nagy 1988, Klaasen et al. 1992), except one on penguins (Gales et al. 1990,). Significant increase or decrease of DEE in tagged birds relative to controls should be a cause for concern, as they indicate that tagged individuals are unlikely to be representative of the population as a whole. An imposed increase in living costs may reduce survival (Culik & Wilson 1991, Daan et al. 1996), whilst a decrease in costs is likely to indicate a reduction of activity (Gales et al. 1990), with probable reduced fitness as a consequence. Combining measures of energy expenditure with behavioural observations allows interpretation of any effect of the tag, and could point to a method for improving transmitter design or attachment.

2. Methods

2.1 ENERGY EXPENDITURE

We measured the energy expenditure of eight takahe (initial mass 2580 ± 132 g (data are given as mean ± SE throughout)), using DLW, over two consecutive periods of three days. These individuals comprised four adults (two females) and four juveniles (all male) On the first period (PERIOD1), four birds (two adults) were fitted with radio transmitters (TAG) and four acted as controls (NOTAG). In the second period (PERIOD2) the treatments were reversed. The transmitters used (mass 48.1 ± 0.8 g; mean percentage of body weight 1.832 ± 0.135%, range 1.39-2.28%) were identical to those used for research on takahe in the Murchison Mountains, and were attached by members of the Department of Conservation team involved there.

The research was conducted at Burwood Bush Research Station, Te Anau, New Zealand, where family groups of takahe live within an electrified boundary fence to protect them from mammalian predators. Takahe were caught by

attracting them into small pens in which the birds were accustomed to receiving supplementary food, by herding them into a net, or by directly grabbing birds in the field where neither of these options was feasible. Only the minimum amount of supplementary feeding necessary to attract birds into a pen was given during the experiment. The DLW technique (Lifson & McClintock 1966, Nagy 1980) following the protocol of Tatner & Bryant (1988) was used to measure energy expenditure. Samples were analysed for stable isotope ratios using mass spectrophotometry. Energy expenditure was calculated from the turnover of deuterium and ^{18}oxygen in the body water (Lifson & McLintock 1966) and using the principles of indirect calorimetry (Brody 1945). For a discussion of the assumptions involved in the DLW technique, see Tatner & Bryant (1988). Takahe were injected intra-peritoneally with DLW (a mixture of 20 APE $H_2^{18}0$, and 99.9 APE ^2H_2O) at 3 μL/gg body mass. Body water content was calculated as 64.9% using the method described in Speakman (1998) and manufacturer's estimates of injectate isotopic composition. The takahe were released into a pen, and re-caught after three hours (this period allowing equilibration of the isotopes in the body water pool). A blood sample (Initial 1) (c. 50 μL) was taken from the tarsal vein, and stored in 10 flame-sealed capillary tubes. Birds were then released. Three days later, the birds were re caught, and a second blood sample was taken (Final 1). Transmitters were removed or attached, and a second injection of DLW (identical to the first) was administered. The birds were released into a pen for 3 hours allowing the new isotopes to equilibrate before being re caught for another blood sample (Initial 2), and released. Finally, the birds were re-caught three days later, another blood sample was taken (Final 2), all transmitters were removed, and the birds were set free. Bird handling was minimised at all times, and birds were released into the pens between procedures. Radio-tags were attached, using a standard backpack design (Maxwell & Jamieson 1997), during the course of the DLW administration procedure. Bird handling times did not differ between TAG and NOTAG treatments (36.6 ± 2.6 min v. 35.8 ± 2.5 min, paired t-test, $t = 0.32$, P < 0.76), nor between Period 1 (Initial 1 to Final 1) and Period 2 (Initial 2 to Final 2) (38.0 ± 2.6 min v. 34.4 ± 2.4 min: paired t-test, $t = 0.54$, P < 0.608).

2.2   BEHAVIOUR

Time budgets of the birds were obtained during the second day of both treatment periods. Behaviour was divided into the following mutually exclusive categories: feeding, standing, walking, running, and preening. Feeding included a small amount of time spent drinking. Walking and running gaits in takahe are quite distinct, and can be easily separated. Time spent preening was further divided into preening apparently focused on the area occupied either by the transmitter or its harness, and the preening of other areas.

2.3 ANALYSIS

All statistical analysis was conducted using Minitab Release 12. All variables used in parametric tests were tested for normality using the Anderson-Darling test, and transformed where necessary (Cohen 1988).

3. Results

3.1 ENERGY EXPENDITURE

Of the 16 DLW samples collected, two were rejected from the analysis: one (TAG) indicated an impossible (negative) value, and the other (NOTAG) an extremely low expenditure (less than one-third of the same bird's TAG expenditure, less than half the next lowest expenditure, and less than two-thirds of the bird's basal metabolic rate as predicted by Aschoff & Pohl's (1970) allometric equation). Both these samples were from juveniles, and both samples showed rapid rates of water turnover likely to make results unreliable, or possibly characteristic of fractionation during storage (Speakman 1998). As a consequence, both were excluded from the analysis, leaving 14 individual samples, but only six repeated measures. Fortunately these comprised three tagged birds in PERIOD1 and PERIOD2, so that the original balanced nature of the experimental design was retained.

Mean TAG daily energy expenditure (DEE) was 1269 ± 153 kJ. This compared with NOTAG DEE of 1179 ± 127 kJ. This difference was significant (paired t-test, $t_5 = 2.69$, $P < 0.044$) and amounted to a 7.7% increase in free-living costs for tagged individuals (Fig. 1). When considering energy expenditure as a multiple of basal metabolic rate predicted from Aschoff & Pohl's (1970) allometric equation for non-passerine birds ($\times BMR_{A\&P}$), a similar significant result was found (TAG $2.00 \pm 0.16 \times BMR_{A\&P}$; NOTAG $1.84 \pm 0.14 \times BMR_{A\&P}$, paired t-test, $t_5 = 3.81$, $P < 0.013$). McNab (1994) measured the basal metabolic rate of takahe directly ($n = 1$), allowing an alternative multiple of basal
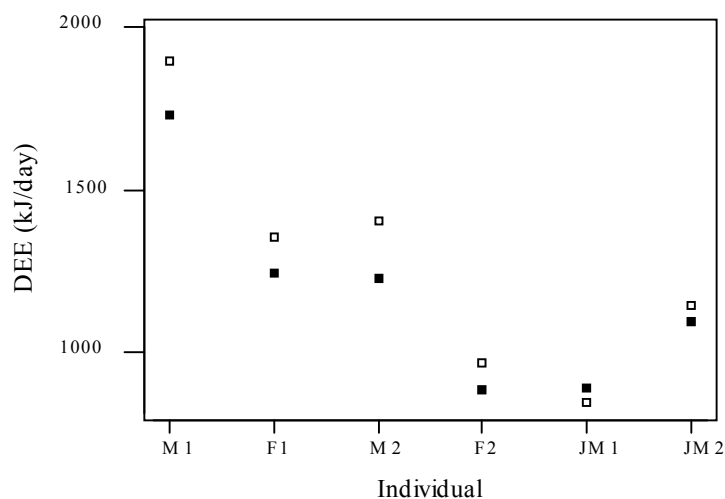

Fig 1. Free-living daily energy expenditure (DEE) for six takahe at Burwood Bush, each measured twice. Open squares represent tagged, closed squares untagged expenditures. Tag-bearing resulted in a significant increase in DEE ($P < 0.05$) of around 8%. M = male, F = female, J = juvenile: F1 and M1 were a pair, and both juveniles were offspring of M2–F2 pair.

metabolism, $\times BMR_{McN}$, to be calculated. This measure yields slightly higher estimates of basal metabolism (Table 1).

No effects due to SEQUENCE of measurement (Period 1 v. Period 2) were detected, indicating no strong effect on energy expenditure of repeated handling. However, SEQUENCE was in any case controlled for by including it as a factor in a general linear model (GLM). This had the effect of slightly reducing the probability of a tag-bearing effect (DEE $P < 0.064$; $\times BMMR_{A\&P}$ $P < 0.019$; $\times BMR_{McN}$ $P < 0.058$).

Mass change (g) (from the start of Period 1 or Period 2 to its end) did not appear to vary with tag-bearing status (GLM entering tag status and individual as factors, time sequence as a covariate, $F_{1,15} = 0.08$, $P > 0.78$). Consequently mass changes independent of tag-bearing could contribute significant variation to expenditure. To account for these effects, MASS CHANGE was entered as a covariate (Table 2), with the effect of increasing confidence that tags were

TABLE 1. MEAN VALUES FOR THREE NON-INDEPENDENT MEASURES OF ENERGY EXPENDITURE IN TAG-BEARING AND UNTAGGED TAKAHE, TOGETHER WITH PAIRED t-TESTS (n = 6 PAIRS).

MEASURE	NOTAG	TAG	t	P
DEE kJ/d	1179 ± 127	1269 ± 153	2.69	0.044
$\times BMR_{A\&P}$	1.84 ± 0.14	2.00 ± 0.16	3.81	0.013
$\times BMR_{McN}$	2.08 ± 0.14	2.23 ± 0.17	2.50	0.055

TABLE 2. GENERAL LINEAR MODEL ANALYSIS OF THE EFFECT OF TAG-BEARING ON THREE NON-INDEPENDENT MEASURES OF ENERGY EXPENDITURE.

GLM entering tag status (TAG v. NOTAG) and individual takahe as factors, with time sequence (PERIOD1 v. PERIOD2), and mass change (mass increase/decrease over the period of measurement).

TERM*		DF	ADJUSTED MEAN SQUARES	F	P
DEE	TAG	1	29327	16.53	0.027
	INDIVIDUAL	5	221726	124.97	0.001
	SEQUENCE	1	9679	5.46	0.102
	MASS CHANGE	1	9918	5.59	0.099
	Error	3	1774		
$\times BMR_{A\&P}$	TAG	1	0.08016	22.84	0.017
	INDIVIDUAL	5	0.23529	67.04	0.003
	SEQUENCE	1	0.01417	4.04	0.138
	MASS CHANGE	1	0.00954	2.72	0.198
	Error	3			
$\times BMR_{McN}$	TAG	1	0.08774	19.99	0.021
	INDIVIDUAL	5	0.23736	54.09	0.004
	SEQUENCE	1	0.04423	10.08	0.051
	MASS CHANGE	1	0.02946	6.71	0.081
	Error	3			

* DEE daily energy expenditure (kJ/d). $\times BMR_{A\&P}$ DEE as multiple basal metabolic rate predicted from the allometric equation of Aschoff & Pohl (1970) for non-passerines. $\times BMR_{McN}$ DEE as a multiple of basal metabolic rate measured by McNab (1994) for single takahe.

indeed affecting energy expenditure (DEE $P < 0.027$; $\times BMR_{A\&P}$ $P < 0.017$; $\times BMR_{McN}$ $P < 0.021$). This model predicted least square mean DEEs of TAG 1274 ± 17 kJ v. NOTAG 1174 ± 17 kJ, amounting to an 8.5% increase due to tags.

Intra-individual variation in energy metabolism was very low compared with inter-individual differences: linear regression of DEE TAG on DEE NOTAG explained almost 97% of the variance (TAG DEE (kJ) = –130 + 1.19* NOTAG DEE (kJ), $F = 159.4$, $P < 0.001$. This slope did not differ significantly from 1 ($T_4 = 2.021$, $P < 0.13$) (Fig. 2). The variation explained by individual is an order of magnitude greater than the variance due to tag-bearing (Fig. 3). This difference was less when aspects of body size were controlled for using xBMR as the energy measure, but even so, the variation due to individual was four times greater than that due to TAG status (Table 2). With inter-individual variation of this magnitude, we would have required a sample size greater than

Figure 2.   Daily energy expenditure of six takahe measured with and without radio-tags. The dotted line represents equality between tag-bearing and non-tag-bearing living costs. Linear regression explains 97% of the variance, $P < 0.001$. The regression slope ($b = 1.19$) does not significantly differ from the dotted line (b = 1) ($P < 0.13$). Intra-individual variation was low; no comparison between tagged and untagged measures differed by more than 14%.
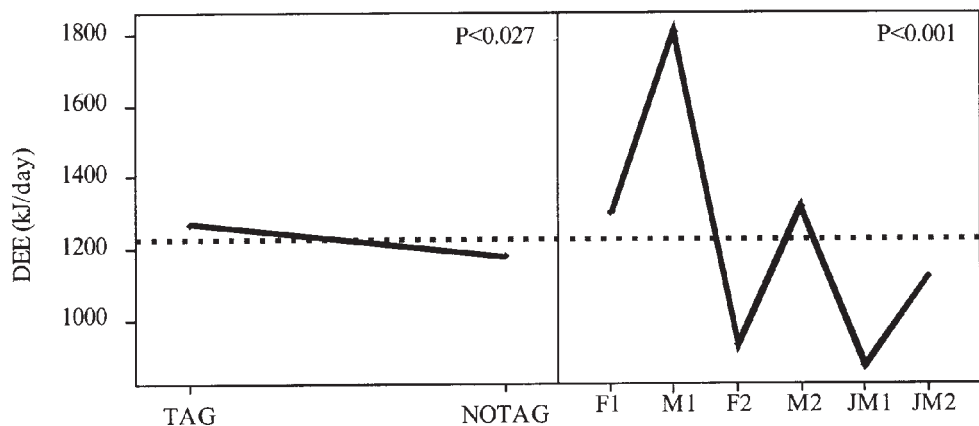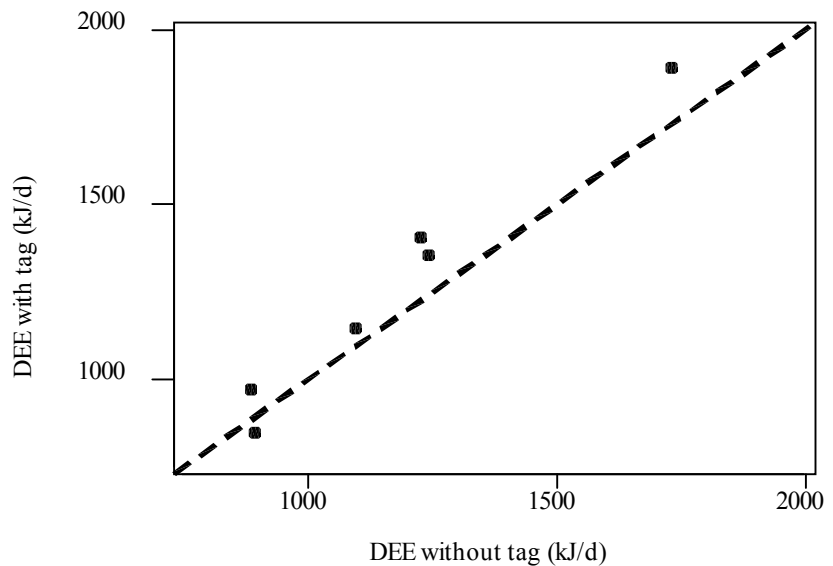

Figure 3.   Relative effect sizes of 'tag-bearing' and 'individual' on daily energy expenditure of six takahe, measured with and without radio-tags. GLM fitted values are used, and the P values refer to the GLM (see Table 2). Individual effects are an order of magnitude greater than tag-effects. F = female, M = male, J = juvenile. F1 and M1 were a pair, both juveniles were chicks from the second pair (F2–M2).

the world population of takahe to have an 80% chance of detecting the effect-size for DEE we found with the repeated measures design.

3.2 BEHAVIOUR

Time budgets of greater than 20 minutes were collected for all individuals, both in TAG and NOTAG treatments, except for one individual for which the tag failed, preventing location in the available time period. Budgets indicated no evidence for a strong effect of tag-bearing on behaviour (Table 3). A GLM incorporating tagged status, individual and time sequence as factors revealed no significant variation in any behaviour (proportion time, arcsine square-root transformed) to be explained by any of these factors (Table 4). Separate GLMs failed to detect any influence of sex or age on time budgets (P > 0.1 in every case). There were no significant correlations between measures of energy expenditure and behaviour.

4. Discussion

4.1 TAG EFFECTS

The DLW methodology was used to provide a quick assay of potential long-term effects of tag-bearing. What it was unable to do, however, was distinguish between the impact of tags in the days immediately following attachment and the impacts after weeks or months of tag-bearing. Since all subjects had their DEE measured in the three days immediately post-attachment, and as none of the birds was habituated to tag-bearing prior to the experiment, there is no reason to expect any confounding of results. Whether tag-effects might decline or increase with time after attachment is worthy of separate investigation.

The cause of elevated energy expenditure in tag-bearing takahe is not entirely clear. The absence of any detectable difference in time budgets when controlling for inter-individual variation suggests that, if tag-bearing modified behaviour, its impact on energy expenditure would probably be small. Similarly it is unlikely that a simple mechanical cost of load-bearing could account for

TABLE 3. TIME BUDGETS FOR TAKAHE AT BURWOOD BUSH.

BEHAVIOUR	PERCENTAGE TIME (± SE)		$P < $ *
	TAGGED	NO TAG	
Feed	75.57 (± 4.06)	75.36 (± 2.44)	0.86
Stand	8.45 (± 1.97)	10.34 (± 2.90)	0.75
Walk	12.12 (± 2.09)	13.82 (± 1.80)	0.96
Run	0.15 (± 0.08)	0.06 (± 0.06)	0.56
Preen	1.72 (± 0.90)	0.42 (± 0.24)	0.38

* P values are from a general linear model (see Table 4)

TABLE 4. GENERAL LINEAR MODEL ANALYSIS OF TIME-BUDGET DATA (ARCSINE-SQUARE-ROOT TRANSFORMED) FOR SEVEN TAKAHE.

Two sets of time budgets were collected for each individual, once while tag-bearing, and once when untagged. TAG status and INDIVIDUAL entered as factors, SEQUENCE entered as a covariate. There was no evidence of a strong effect of tag-bearing on behaviour.

TERM*		DF	ADJUSTED MEAN SQUARES	F	P
%FEED	TAG	1	0.00044	0.03	0.862
	INDIVIDUAL	6	0.01209	0.91	0.564
	SEQUENCE	1	0.00555	0.42	0.547
	Error	5	0.01334		
%STAND	TAG	1	0.00209	0.11	0.754
	INDIVIDUAL	6	0.00592	0.31	0.920
	SEQUENCE	1	0.03013	1.58	0.264
	Error	5	0.01906		
%WALK	TAG	1	0.00001	0.00	0.959
	INDIVIDUAL	6	0.01017	2.04	0.224
	SEQUENCE	1	0.00242	0.49	0.516
	Error	5	0.01241		
%RUN	TAG	1	0.00051	0.39	0.560
	INDIVIDUAL	6	0.00054	0.39	0.858
	SEQUENCE	1	0.00034	0.26	0.634
	Error	5	0.00130		
%PREEN	TAG	1	0.00605	0.94	0.376
	INDIVIDUAL	6	0.00868	1.35	0.383
	SEQUENCE	1	0.00097	0.15	0.713
	Error	5	0.00642		

more than a portion of the increase in DEE. Taylor et al. (1980) have shown a direct proportionality between locomotion cost and load size, so that the mean increase in energy expenditure whilst supporting body (plus tag) weight for takahe in this experiment would be equal to the mean percentage body mass represented by the tag (= 1.83%). However, when the bird was not actively supporting its body (e.g. roosting), reduced impact of the tag on muscle activity would be expected, and hence the overall DEE increase due to the mechanical cost of tag-bearing should be less than 1.83%.

Using our daytime budgets of takahe at Burwood Bush, and following the logic of Pandolf et al. (1977) and Taylor et al. (1980), we estimate that a maximum of 15% of the observed increased in DEE could be attributed to the costs of mechanically supporting and transporting the load. Furthermore, if muscular support of the tag mass were an important component of the increased costs, we would anticipate a positive relationship between percentage increase in DEE whilst tag-bearing on the one hand and percentage body mass that the tag represented. In fact the relationship showed a negative tendency ($r_s = -0.906$, $P < 0.012$) when linearised using the antilog of percentage body mass), suggesting that smaller (juvenile) birds were less affected by tag bearing than

were adults. This accords with the slope of the relationship shown in Fig 2, though this did not significantly differ from 1.0.

4.2   HEAT LOSS

If the tag and its backpack harness caused feather disruption, it could transfer heat to the environment. Previous studies have shown both the abrasive effects of harnesses on birds (Buehler et al. 1995) and the potential for heat loss via dorsally sited tags (Bakken et al. 1996). Although the tags we used appeared to be completely covered by outer feathers, they felt warm to the touch on removal. This was taken to indicate that some heat transfer was occurring. Heat transfer can be expected to increase proportionately with the difference between ambient temperature and body temperature. The temperatures encountered during this study ranged from 3.9 to 18.7°C, mean 10.9°C, i.e. considerably warmer than winter temperatures experienced by wild birds in the Murchison Mountains (mean 1973–94, –0.3 ± 0.8°C (Maxwell & Jamieson 1997)). The estimate of increased energy expenditure at Burwood Bush due to tags should be regarded as conservative for costs in winter conditions in the Murchison Mountainss.

If heat transfer costs are indeed responsible for a significant portion of tag-dependent costs, it is probable that the greatest impact of tags will occur when energy balance is in any case most difficult to achieve, i.e. in cold winter conditions (Maxwell & Jamieson 1997). Consequently, variation in expenditure due to tag-bearing could have important fitness consequences for wild takahe.

Although there was marked inter-individual variation in DEE (in part due to large variation in body size), intra-individual variation was very low. High repeatability in takahe DEE suggests possible inflexibility in energy budget; if birds spend a high proportion of their time feeding, they would not have much scope for modifying their energy intake rate in response to increased costs. Under these circumstances the observed 7.7% increase in DEE might be significant, particularly if this turns out to be an underestimate of the increase during the most severe conditions.

5.   Conclusions

If thermoregulatory costs are indeed a significant component of increased energy costs induced by radio-tagging in the takahe, there are several ways in which the impact could be moderated by tag design:

- reducing tag size (in all three dimensions);
- restricting use to warmer seasons;
- positioning the tag on the tail or wing where it is less likely to promote heat loss;
- incorporating a layer of air at the base of the tag to increase insulation;

- silvering the tags to minimise heat loss via radiation (at present tags are apparently highly efficient black radiators).

Whilst the first three of these would be likely to reduce the scope of effectiveness of current research into causes of takahe mortality, the fourth and particularly the last could be achieved with relatively little financial outlay.

Despite being constrained in the number of takahe available for analysis, in part by their scarcity, and in part by a reasonable reluctance on the part of conservation managers to allow larger numbers of birds to be disturbed, we were able to detect significant effects of tag-bearing on energy expenditure. However, shortage of data points is likely to be a recurring problem in assessing the costs of tag-bearing in endangered animals. Repeated measures designs are more powerful than simple ANOVAs, and offer the best ratio of power to sample size, but these are often difficult to achieve in animal ecology, unless a study can be laboratory- or aviary-based, which is unlikely for endangered species. Managers will then, often be left with the conundrum of what to do with low-power results. We address these issues in our review of radio-tracking studies of the last decade (Godfrey & Bryant 2003).

6. Acknowledgements

7. References

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