

Energetics of blue ducks in rivers of differing physical and biological characteristics

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ABSTRACT

The relationship between habitat structure, habitat quality and energy expenditure was investigated in free-living blue ducks (*Hymenolaimus malacorhynchos*). Daily energy expenditure was strongly related to territory size, and, when controlling for this, negatively related to altitude. Relatively long territories were associated with high living costs amongst ducks on natural-flow catchments. Ducks on regulated-flow rivers had relatively high costs in relation to their territory lengths, because despite having significantly shorter territories than birds from natural catchments, their living costs were similar. Energy expenditure was not directly related to measured aspects of habitat structure (including catchment vegetation, channel size and gradient) nor to any available index of habitat quality (breeding density, proportion breeding, juvenile production per year). To account for these results, we model living costs as a combination of foraging costs and territorial defence costs. Traditional models of territory economics may be inappropriate for analysis of blue duck territories because the direct connection between area and defence need not apply to a linear territory with only two points of access. We suggest that defence costs vary negatively with territory length, whilst foraging costs are positively related to territory size. The ultra-short territories of birds on regulated-flow rivers may impose higher territory defence costs than occur in unmodified habitats. Our measurements indicate that habitat quality depends on resource density, which may be assessed by estimating territory length. However, rivers supporting territories of intermediate lengths, where blue ducks typically have low energy expenditures, may offer the best chance of sustaining blue duck populations into the future.

Keywords: energy expenditure, habitat quality, habitat assessment, territoriality, foraging, blue ducks, *Hymenolaimus malacorhynchos*.

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Godfrey, J.D.; Bryant, D.M.; Williams, M. 2003: Energetics of blue ducks in rivers of differing physical and biological characteristics. Pp. 35-68 *in*: Williams, M. (Comp.) 2003: Conservation applications of measuring energy expenditure of New Zealand birds: Assessing habitat quality and costs of carrying radio transmitters *Science for Conservation* 214. 95 p.

1. Introduction

The blue duck (*Hymenolaimus malacorhynchos*) is a riverine specialist endemic to New Zealand. It is classified as 'threatened', with an estimated population size of 2000–4000 (Bell 1986). Monitoring population size and reproductive performance has been a significant component in the development of a conservation strategy for the blue duck (Williams 1988, Adams et al. 1996). As a result, some of the measures that have been traditionally employed to assess habitat quality, namely density and breeding success, are better known for this avian species than for any other in New Zealand, except perhaps a few 'flagship' conservation species. Unfortunately, rather less is known regarding juvenile and adult survival, which are also integral to population viability.

The range of the blue duck is believed to have contracted considerably in historical time, leaving the bird restricted to forested upland rivers in the North Island, and to the largely unmodified habitats of the west of the South Island (Fordyce 1976, Bull et al. 1985; Cunningham 1991). Blue ducks are nevertheless represented in a range of physically and geographically diverse habitats. Accordingly, this species offers the best opportunity amongst New Zealand birds to seek a relationship between habitat structure, habitat quality and the energy expenditure of individuals occupying it.

Previous studies of blue ducks have focused principally on the rivers of the North Island, on aspects of food supply and foraging ecology (Collier 1991; Collier & Lyon 1991, Veltman et al. 1991, 1995; Collier & Wakelin 1996), territoriality (Eldridge 1986; Veltman & Williams 1990), social demography (Williams 1991; Triggs et al. 1992; Veltman et al. 1991; Williams & McKinney 1996) and on distribution (Collier et al. 1993). Attempts to advance conservation planning by synthesising thinking on territoriality, foraging and breeding success have been few, but Veltman et al. (1991) argued that territories may not be defended as a food resource, but instead function to guard mates. However, a study exploring the distribution of blue ducks (Collier et al. 1993) found that several aspects of river morphology and prey species were associated with the presence/absence of breeding ducks. This suggests that resources play an important role in blue duck distribution, and therefore probably in territoriality and population structure. Any understanding of the conservation needs of this species must therefore include an analysis of resource-based variation in habitat quality.

Accordingly, we explore interactions between blue ducks and their habitat via free-living energy expenditure within a framework of territory economics. We test the hypothesis that favourable habitat provides a double saving in energy expenditure: high foraging returns and low maintenance costs, and hence that a negative relationship exists between habitat quality and living costs.

2. Methods

2.1 SAMPLING

We selected rivers in both the North and South Islands where pre-existing data pertaining to their quality as blue duck habitat were available (Tables 1, 2). These rivers were in both natural-flow and regulated-flow catchments. We attempted to measure the energy expenditure of two pairs of ducks from each river, principally during the non-breeding period. To compensate for missing data points regarding habitat quality, we ranked Habitat quality (on a three-point scale, 1 = good, 2 = intermediate, 3 = poor) based on the available data. In ranking the rivers we used firstly juvenile production/km/year, and secondly pair density, to assign quality rank, and attempted to distribute ranks equally, ending with four rivers ranked 1, four ranked 2, and five ranked 3 (including two rivers sustaining only single birds (Table 2)).

Birds were caught either by using nets set up across the river channel, or, at night, by a combination of bright lights and hand-nets. Occasionally, radio-tagged birds could be located at a roost, where it was possible to grab them by hand, or to net the exits. Birds were weighed (± 5 g) using a hand-held Pesola balance, and their tarsi, head + bills, and keels were measured (± 0.1 mm) using callipers.

TABLE 1. LOCATION AND CHARACTERISTICS OF SAMPLED RIVERS.

River	Position	Natural/ regulated	Channel size (points)*	Mean gradient (m/km) [†]	Altitude (m a.s.l.)	Catchment vegetation cover (%) [‡]			
						Bush	Scrub	Pasture	Alpine
Takaputahi	38° 8'S, 177° 35'E	nat	3	4	315	85	5	10	0
Okuputa/ Mangatepopo	39° 2'S, 175° 32'E	reg	2	15	480	70	10	10	10
Whakapapa	39° 8'S, 175° 28'E	reg	5	22	670	40	5	40	15
Tongariro	39° 11'S, 175° 49'E	reg	5	15	665	30	15	0	55
Waiwhakaiho	39° 14'S, 175° 32'E	nat	3	28	480	70	15	0	15
Manganui	39° 14'S, 175° 32'E	nat	3	50	645	60	20	0	20
Upper Manganui-a-te-ao	39° 17'S, 175° 21'E	nat	4	40	610	70	0	0	30
Manganui-a-te-ao	39° 20'S, 175° 14'E	nat	5	20	325	50-70	0	20-40	10
Apias	39° 37'S, 176° 15'E	nat	1-2	30	750	90	0	0	10
Makaroro	38° 39'S, 176° 14'E	nat	1	15	730	95	5	0	0
Flora Stream	41° 11'S, 172° 44'E	nat	1	50	915	100	0	0	0
Edwards	42° 55'S, 171° 40'E	nat	1-2	25	1080	0	5	0	95
Perth River, Whataroa	43° 20'S, 170° 28'E	nat	5	15	395	70	0	0	30
Clinton	44° 53'S, 167° 49'E	nat	3	18	340	25-50	10-25	0	40-50

* Ranked scale of channel width, using means of multiple point estimates: 1 = < 2.5m; 2 = 2.5-5.0 m; 3 = 5-10 m; 4 = 10-20 m; 5 = > 20 m. All estimates by J.D.G. except Takaputahi by M.J.W.

† Estimated from 1:50 000 maps, using the mean of individual blue duck territories.

‡ Percentage land use estimated to nearest 5% from 1:50 000 maps according to the definitions therein. All bush is natural/semi-natural except 10% forestry at the Okuputa River. 'Alpine' refers to unfarmed land above the tree/scrub line. Where a range is given, it shows extent of variation between territories on a single river.

TABLE 2. AVAILABLE REPRODUCTIVE AND POPULATION DENSITY DATA FOR BLUE DUCK AT THE SITES USED IN THIS STUDY.

River	Max. density (pairs/km)	Mean density (pairs/km)	Juveniles (/km/y)	Juveniles (/pair)	Pairs breeding (%)	Habitat quality rank	Source
Takaputahi	0.42	0.29	0.52	1.74	*	2	M.J.Williams (unpubl. data)
Okuputa/ Mangatepopo	2.67	1.62	0.95	0.59	0.23	1	Tongariro/Taupo Cons.
Whakapapa	1.29	0.96	1.36	1.40	0.45	1	Tongariro/Taupo Cons.
Tongariro	0.85	0.59	0.70	1.10	0.40	2	Tongariro/Taupo Cons.
Waiwhakaiho [†]	0	0	0	0	0	3	Taranaki Conservancy
Manganui [†]	0	0	0	0	0	3	Taranaki Conservancy
Upper Manganui-a-te-ao	0.75	0.43	0.25	0.59	*	2	K.Oates (unpubl. data)
Manganui-a-te-ao	1.08	0.78	0.90	1.11	0.84	1	M.J.Williams (unpubl. data)
Apias	0.615	0.46	0.26	0.61	0.29	2	J.Adams (unpubl. data)
Makaroro	0.385	0.25	0.18	0.78	0.22	3	J.Adams (unpubl. data)
Flora Stream	0.923	0.62	*	*	0.50	1	Shaw (1996)
Edwards	0.67	0.33	0.20	*	0.50	3	M.A.Harding (unpubl. data)
Clinton	*	0.20	*	*	*	3	This study

* No data available.

[†] Introduced population, only males present.

2.2 ENERGETICS

Free-living energy expenditure was measured using the doubly labelled water (DLW) technique (Lifson & McClintock 1966; Nagy 1980; Bryant & Tatner 1988; Tatner & Bryant 1988; Speakman 1997) This technique involves capture of the focal animal, the injection of stable (i.e. non-radioactive) isotopes of hydrogen (²H) and oxygen (¹⁸O) in the form of water, and a period of restraint allowing equilibration of the isotopes in the body water pool before taking a sample of the initial isotopic enrichment levels of the body water. This is normally taken in the form of blood (c. 0.1ml). 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), and a review of strengths and weaknesses of the DLW technique is given in Williams & Vezina (2001).

2.3 DLW FIELD PROTOCOL

Immediately after capture and weighing, ducks were injected with DLW at 5 $\mu\text{L/g}$ body mass. Injection was intra-peritoneal, and the injectate was made up from 20.0 APE H_2^{18}O and 99.8 APE $^2\text{H}_2\text{O}$. Following a 120 min equilibration period, during which ducks sat quietly in shaded bird-bags, a blood sample consisting of c. $10 \times 5 \mu\text{L}$ capillary tubes was taken from the tarsal vein. Capillary tubes were immediately flame-sealed, and birds were released onto their territories.

Individuals were re-caught approximately 48 ($n = 8$), 72 ($n = 14$), or 96 ($n = 18$) hours after the initial release, and, after weighing, a second blood sample was taken in the same manner as the first, using the other tarsal vein, and the birds immediately released.

DLW samples from 13 sites were obtained from December 1997 to May 1998, and from November 1998 to Jan 1999. Thirty-nine individuals were sampled, comprising 24 males and 15 females. Three of the females were sampled on two occasions (2.5, 6.5, and 12 months apart), and one male has been discarded from the energetics analysis because of damaged samples. A total of 40 energetics measures were available, 23 from males and 17 from females (Table 3). These comprised 10 breeding birds (all at the chick-rearing stage) and 30 non-breeding birds, of which nine birds were moulting, three were assumed to be pre-moult, and 18 post-moult. Biometric measures alone were available for a further 14 males (four moult, 11 post-moult) and six females (one moult, five post-moult).

2.4 RADIO-TRACKING

A small radio-tag (Sirtrack Ltd., mean mass 2.63 ± 0.02 g) representing 0.2-0.4% body mass was attached to each duck. The tag was glued and tied to the dorsal surface of a central tail-feather, near the base, using a combination of quick-drying 'superglue' adhesive and dental floss. The aerial was tied at several points along the retriex, with the tip extending about 1 cm past the end of the feather. The upper tail coverts covered the body of the tag completely.

Birds were followed using a hand-held Yagi aerial and a Telonics TR4 receiver during the course of the DLW measurements. Observers remained hidden from the ducks, using riparian cover. Duration of tracking periods varied from 5 to 10 hours, over a course of 2 to 3 days. In each case an approximation of territory area was obtained, based on radio-locations and direct observations, and transcribed on to 1:50 000 series maps. Territory size is expressed not as area, but as length of channel, and this was calculated to the nearest 50 m from the maps.

TABLE 3. DETAILS OF INDIVIDUAL BODY SIZE AND ENERGY EXPENDITURE OF BLUE DUCKS ON DIFFERENT RIVERS.

BIRD NO.	RIVER	SEX	STATUS	DEE (kJ/h)	×BMR*	MASS (g)	TARSUS (mm)	PAIRED/SINGLE
1	Manganui-a-te-ao	F	breeding	496	2.36	710	47.3	P
2	Manganui-a-te-ao	M	breeding	912	3.65	844	52.1	P
3	Manganui-a-te-ao	F	breeding	437	2.07	714	50.0	P
4	Manganui-a-te-ao	M	breeding	369	1.50	833	50.0	P
5	Manganui-a-te-ao	F	breeding	478	2.24	720	47.5	P
6	Manganui-a-te-ao	M	breeding	623	2.50	842	51.1	P
7	Manganui-a-te-ao	F	breeding	869	4.59	639	46.8	P
8	Manganui-a-te-ao	M	breeding	923	3.61	865	50.9	P
1	Manganui-a-te-ao	F	moult	521	2.19	805	47.4	P
5	Manganui-a-te-ao	F	moult	585	2.42	815	48.2	P
9	Apias	M	moult	603	2.26	904	52.7	P
10	Apias	M	moult	566	2.01	950	51.7	P
11	Apias	F	moult	611	2.79	740	47.6	P
12	Tongariro	M	post-moult	428	1.53	945	51.3	P
13	Tongariro	F	post-moult	334	1.44	785	46.0	P
14	Tongariro	M	post-moult	722	2.38	1025	49.5	P
15	Flora Stream	F	post-moult	442	1.99	750	45.0	P
16	Flora Stream	M	post-moult	540	1.69	1078	50.0	P
17	Okuputa	M	post-moult	723	2.71	900	44.8	P
18	Okuputa/Mangatepopo	F	post-moult	614	2.32	895	46.3	S
19	Makaroro	F	post-moult	444	2.03	738	49.0	P
20	Makaroro	M	post-moult	686	2.28	1015	51.0	P
21	Waiwhakaihō	M	post-moult	681	2.77	830	52.2	S
22	Manganui	M	post-moult	812	2.80	980	52.2	S
23	Takaputahi	M	post-moult	*	*	855	51.3	P
24	Takaputahi	F	post-moult	663	2.75	815	49.2	P
25	Takaputahi	F	post-moult	349	1.75	675	41.3	P
26	Takaputahi	M	post-moult	428	1.64	883	50.3	P
27	Whakapapa	M	post-moult	682	2.40	960	51.5	P
28	Whakapapa	F	post-moult	426	1.67	863	46.8	P
29	Whakapapa	M	post-moult	692	2.44	960	48.6	P
30	Upper Manganui-a-te-ao	M	post-moult	611	2.39	863	49.3	P
31	Whakapapa	M	pre-moult	685	2.68	863	50.6	S
28	Whakapapa	F	moult	707	3.07	780	47.4	P
32	Edwards	M	breeding	905	3.03	1010	52.6	P
33	Edwards	F	breeding	707	2.77	863	46.8	P
34	Edwards	M	pre-moult	515	1.71	1018	53.2	S
35	Clinton	M	pre-moult	793	2.32	1155	52.3	P
36	Clinton	M	moult	621	2.23	940	52.6	P
37	Clinton	F	moult	499	1.69	998	48.9	P
38	Clinton	M	moult	995	2.93	1150	54.5	P
Mean				617.4	2.391	877.2	49.4	
SE				26.5	0.102	19.0	0.43	
<i>n</i>				40	40	41	41	

* Energy expenditure as a multiple of basal metabolic rate, using McNab's (1994) estimate.

2.5 TIME BUDGETS

Time budgets were collected for 10 pairs of ducks, simultaneously recording the behaviour of both pair members. Ducks were observed from cover at the sides of river channels, and data were discarded if ducks appeared to detect observers. After such a disturbance, a period of 10 minutes following settling was allowed before behaviour was recorded again. Point samples were taken at 60 s intervals, using a timer-signal, and the bird's behaviour at that instant was defined as one of the behavioural categories described in Veltman & Williams (1990). These were later grouped into one of the following mutually exclusive categories: feeding, locomotion, resting, preening and fighting. When a bird was out of sight at one of the 60s intervals, no behaviour was recorded. We took the proportion of scores for each category to equal the proportion of time spent by ducks engaged in that behaviour.

Radio-tracking and night-vision equipment were used in an effort to determine nocturnal time-budgets for ducks.

2.6 ENVIRONMENTAL VARIABLES

Daily maximum and minimum riverside shade temperatures were taken (c. 1 m above ground) during the course of the DLW measurements.

Several estimates of channel width were made at semi-randomly distributed points along a territory. On the basis of the means of these estimates, channel width for each territory was ranked as follows: rank 1, < 2.5 m; rank 2, 2.6–5.0 m; rank 3, 5.1–10.0 m; rank 4, 10.1–15.0 m; rank 5, > 15.0 m (Table 1).

Some aspects of the physical environment were determined for each territory from 1:50 000 maps: mean territory gradient (m rise/km); median territory altitude (m); territory streamside bush (%); territory streamside scrub (%); catchment bush (%); catchment scrub (%); catchment forestry (%); catchment pasture (%); and catchment alpine grassland (%). In addition, latitude and longitude were recorded for each territory (Table 1).

2.7 ANALYSIS

Restricted Maximum Likelihood (REML) in Genstat (Genstat 5 Committee 1993) was used to analyse cross-river data. This procedure allows mixed effect models (i.e. incorporating random and fixed effects) to be used on non-orthogonal, unbalanced data sets, so avoiding pseudo-replication (Hurlbert 1984). Where analysis was not complicated by pseudo-replication, General Linear Models (GLM) (Minitab Release 12) were used. Normal probability distributions of residuals from both REML and GLM models were examined to check for violation of model assumptions. Catchment habitat characteristics were summarised using Principal Components Analysis in Minitab (Release 12). Throughout, where parametric statistics are used, data have been normalised by transformation where necessary. The proportions from the time-budget data

were transformed using arcsine-square-root before analysis. Means are given \pm SE unless otherwise stated. Local regression (loess) (in S-Plus 2000, Release 1, MathSoft Inc.), essentially a non-parametric smoothing function using locally-weighted least-squares, was used to characterise non-linear relationships.

3. Results

3.1 ENERGY EXPENDITURE

Mean daily expenditure of 40 blue ducks (23 male, 17 female; see Table 3) was 617 ± 26.5 kJ/d. Expressed as a multiple of basal metabolic rate, using McNab's (1994) estimate, mean expenditure was $2.39 \pm 0.10 \times \text{BMR}$. A slightly lower figure is obtained if Aschoff & Pohl's (1970) conventional allometric equation for non-passerines is used to predict BMR ($= 2.20 \pm 0.09 \times \text{BMR}$).

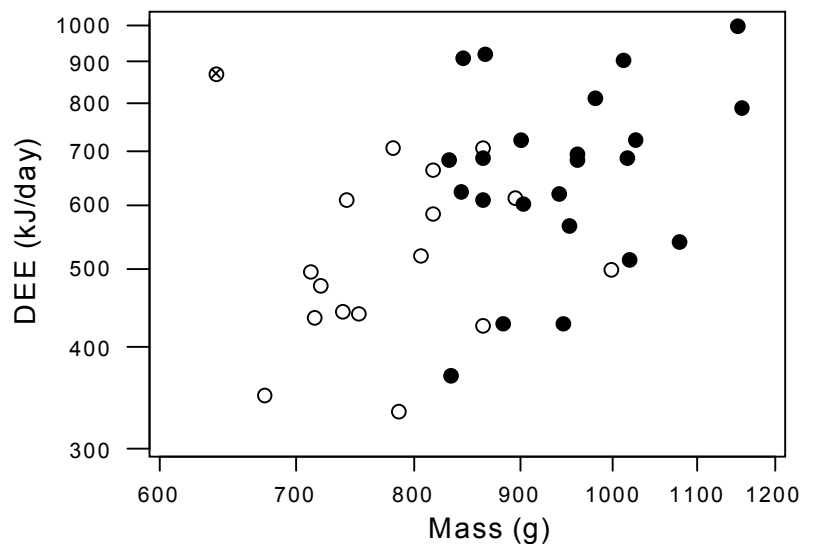
Males were significantly larger than females, and had significantly higher daily energy expenditures, but when size was controlled for by expressing DEE as a multiple of BMR, there was no detectable difference due to sex (Table 4). As is commonly reported for other species (Bryant 1997), body mass of blue duck was a significant predictor of their energy metabolism, explaining up to 27% of the variation in DEE (Fig. 1). Using the entire data set, the exponent of logDEE and logMass relationship was 0.78, close to scalings (0.7 to 0.8) reported for interspecific comparisons (Nagy 1987). Intra-specific exponents are more contentious, however, and removal of one outlier from this relationship (no. 7, Table 3) led to a new slope of 1.07. This new slope did not differ significantly from either 0.80 ($t_{37} = 0.93$, $P < 0.8$), or 0.7 ($t_{37} = 1.28$, $P < 0.4$).

TABLE 4. SEX DIFFERENCES IN SIZE AND ENERGY EXPENDITURE OF BLUE DUCK.

	MALE (mean \pm SE)	FEMALE* (mean \pm SE)	DF	<i>t</i>	<i>P</i>
Mass (g)	944.3 \pm 19.4	781.1 \pm 24.4	36	5.13	0.0001
Tarsus (mm)	51.1 \pm 0.4	47.0 \pm 0.5	36	6.14	0.0001
Head and bill (mm)	96.0 \pm 0.4	88.0 \pm 0.5	36	6.82	0.0001
Keel (mm)	96.0 \pm 0.9	88.2 \pm 0.9	35	6.16	0.0001
DEE (kJ/d)	674.5 \pm 34.4	540.1 \pm 34.3	38	2.72	0.01
$\times \text{BMR}$	2.41 \pm 0.12	2.36 \pm 0.18	38	0.24	0.81

* Three individuals were measured twice (one measured in different years, two at different breeding stages). These are treated as independent for energy expenditure measures, but not for measurements of size and weight, where the second measure was excluded in each case.

Figure 1. Influence of body mass on energy expenditure on the daily energy expenditure of blue duck, plotted on log scales. Females, open circles; males, filled circles. Linear regression explains 16% of the variance with the equation: $\log DEE \text{ (kJ/d)} = 0.483 + 0.78 \log \text{Mass (g)}$. Exclusion of the outlier (marked with a cross) changed the regression equation to: $\log DEE \text{ (kJ/d)} = 0.374 + 1.07 \log \text{Mass (g)}$, $s = 0.103$, $n = 40$, $P < 0.001$, and the variance explained to 27%. Neither slope differs significantly from 0.7 or 1.0.



3.2 HABITAT QUALITY

The mean reported density of pairs in a catchment was positively correlated with the mean reported total production of juveniles/km (linear regression, $\log \text{Number of juveniles (km/year)} = -0.058 + 1.00 \log \text{Density (pairs/km)}$, $n = 9$, $s = 0.208$, $r^2 = 65.2\%$, $F_{1,7} = 13.09$, $P < 0.009$, Fig. 2). The slope of the line was 1.00, indicating that juvenile production was directly proportional to pair density. In the absence of any information regarding adult survival, this justifies the assumption that population density is directly related to habitat quality, and that high-density populations of blue duck are not simply a sink for excess birds (Van Horne 1983). The absence of strong negative relationships between mean pair density and either mean proportion of pairs making a breeding attempt ($r_7 = 0.12$, $P < 0.78$) or mean number of fledged juveniles produced per pair ($r_7 = -0.16$, $P < 0.70$) tends to support this view. These data are consistent with the predictions of the Ideal Free Distribution (Fretwell & Lucas 1970), under which individuals experience similar fitness across a range of habitats of differing quality. However, the impact, if any, of density on adult survival remains unknown.

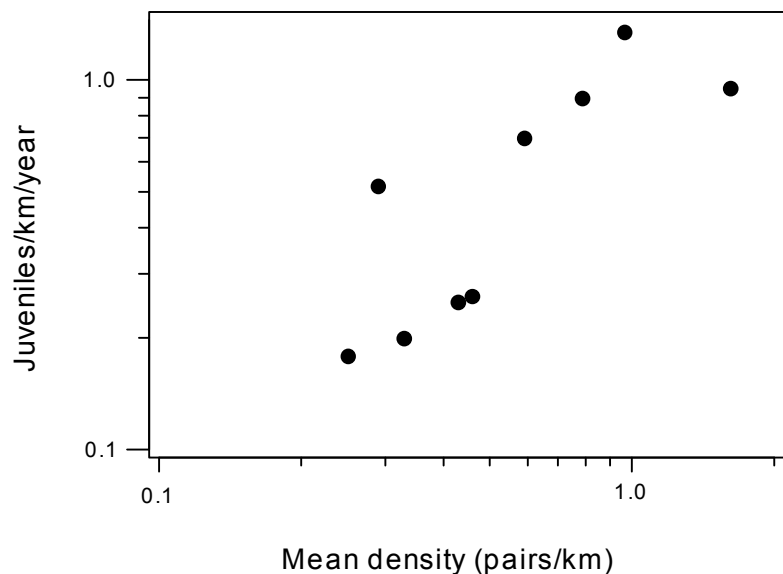
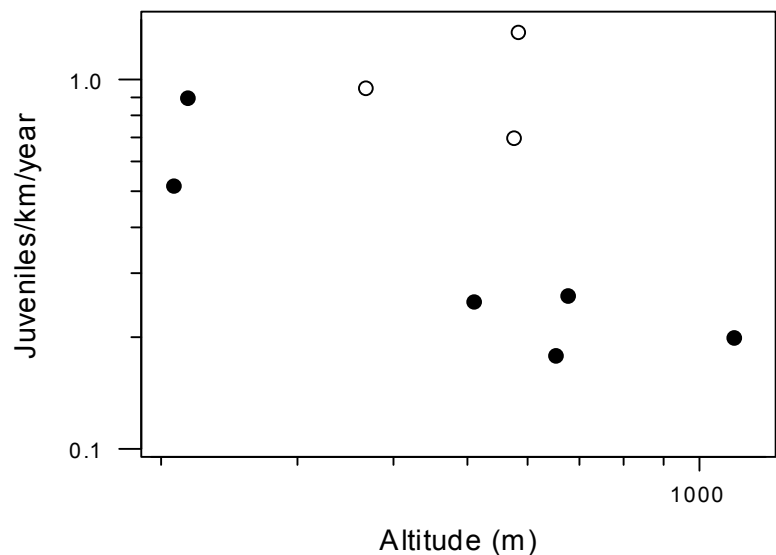


Figure 2. Relationship between mean fledged juvenile production/km/yr and mean pair density of blue duck from nine catchments (excluding two where only single birds were found (Table 2)). Juvenile production is proportionately related to pair density.

Mean pair density, and mean juvenile production/km/year were related to the nature of catchment hydrology, with each being significantly greater amongst rivers with regulated-flow (ANOVAs of log-transformed data excluding catchments with no pairs: mean pair density $F_{1,9} = 8.54$, $P < 0.017$; juveniles/km/year $F_{1,7} = 7.80$, $P < 0.027$). That these differences are detectable from a sample of only three regulated-flow rivers implies a strong effect, but suggests caution regarding causality, particularly because the three regulated rivers are geographically close to each other (Table 1). General linear models were constructed for mean pair density and juvenile production (both log-transformed). These identified catchment hydrology as a significant predictor in each case ($P < 0.013$ and $P < 0.003$ respectively), having discarded measures of channel size, catchment bush, and mean river gradient. Regulated-flow rivers had significantly higher predicted mean production of juveniles and significantly higher mean density of pairs than natural-flow rivers (back-transformed means: juvenile production (number/km/year) 0.99 on regulated, 0.32 on natural; pair density (pairs/km) 0.97 on regulated, 0.38 on natural). Altitude (log-transformed) was negatively related to production when controlling for hydrology ($P < 0.012$; Fig. 3) but had no impact on pair density ($P < 0.98$), possibly suggesting that at higher altitudes individuals experienced lower mean fitness.

Figure 3. Mean juvenile production of blue ducks as a function of mean river altitude. Natural-flow rivers, filled circles; regulated-flow rivers, open circles. Two rivers where only single birds were found have been excluded (Table 2). For natural-flow rivers alone the relationship is significant: $\log \text{Juvenile production} = 2.65 - 1.14 \log \text{Altitude}$, $n = 6$ rivers, $r^2 = 80.5$, $s = 0.134$, $F_{1,4} = 16.53$, $P < 0.015$). When the regulated-flow rivers are included, the relationship is not significant, $F_{1,7} = 2.76$, $P < 0.14$, but GLM ANOVA of the whole data set shows a significant negative effect of altitude when controlling for hydrology ($P < 0.012$).



3.3 TERRITORY SIZE

Blue duck territories varied in length from 400 to 2400 m, with a median of 1000 m. Amongst those territories for which the data were available, there was no correlation between duration of observation and estimated territory length ($r_{18} = -0.14$, $P < 0.7$), suggesting that sufficient effort was made to determine territory size. We obtained an estimate of territory length from both pair members, but to avoid pseudo-replication, we analysed territory length by territory, rather than by individual bird. Because blue duck pairs maintain close contact with each other throughout the day, estimated territory lengths for pair

members tended to be identical. Where this was not the case (one instance) the territory of the pair was taken to equal the longest individual estimate. Considered simply, territories were shorter on regulated-flow rivers (ANOVA: $F_{1,23} = 17.02$, $P < 0.001$). However, the difference between regulated and non-regulated river territories emerged fully only when controlling for altitude (Fig. 4). Including regulated flow rivers, $\log\text{Territory length} = 2.11 + 0.325 \log\text{Altitude}$: $n = 25$, $s = 0.224$, $r^2 = 7.0$, $F_{1,23} = 1.73$, $P < 0.202$. When regulated river territories were excluded from the analysis, up to 60% of the variance in territory length was attributable to altitude according to the regression equation $\log\text{Territory length} = 1.48 + 0.602 \log\text{Altitude}$ ($n = 18$ territories, $s = 0.106$, $r^2 = 60.4$, $F_{1,16} = 24.37$, $P < 0.001$). Birds on regulated-flow rivers had territories 30-50% of the length predicted by this regression.

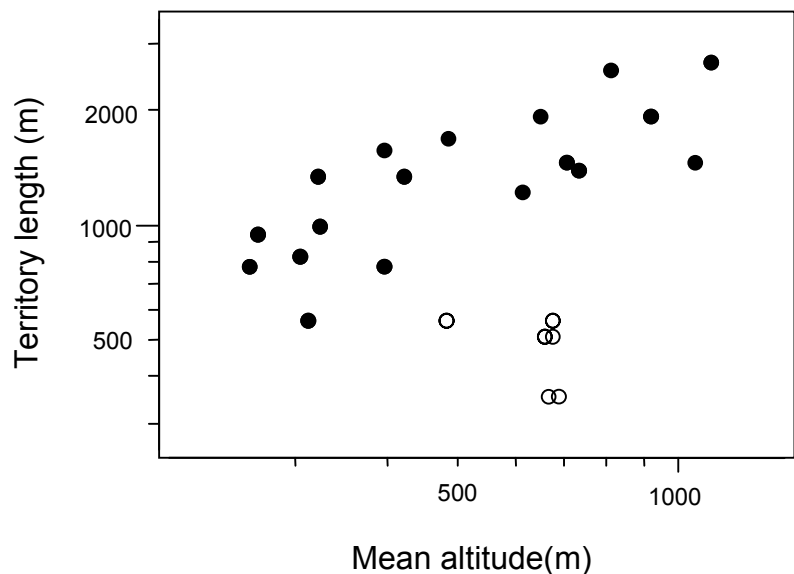


Figure 4. Relationship between territory length and mean territory altitude for blue ducks from different rivers. Natural-flow rivers, filled circles; regulated-flow rivers, open circles. Each territory appears only once, despite both pair members frequently being sampled.

3.4 BODY CONDITION

Body mass was highly correlated with tarsus length: $\text{mass (g)} = -607 + 30.3 \text{ tarsus (mm)}$: $s = 108.9$, $r^2 = 36.6$, $P < 0.001$, $n = 61$ (Fig. 5)). Residual variation in mass not explained by reference to structural size can be used to characterise body condition (Jakob et al. 1996), although fatness should not necessarily be regarded as a correlate of fitness (Witter & Cuthill 1993). The mass-tarsus residual was used as the response variable in a REML analysis, entering RIVER as a random effect (Table 5). FLOW (whether the catchment was of natural or regulated flow), ISLAND (North v. South), SEX, and STAGE (stage of the yearly cycle: breeding; moult; or post/pre-moult) emerged as significant predictors. Males ($P < 0.001$), birds on regulated-flow rivers ($P < 0.001$, Fig. 6), and South Island birds ($P < 0.001$) were relatively heavy for their structural size, whilst breeding birds were significantly lighter than moulting or post-moult birds ($P < 0.003$, Fig. 7). Replacing the factor ISLAND with the covariate LATITUDE in this model led to an increase in residual deviance, suggesting a categorical difference in body condition between North and South Island birds, rather than a clinal change with latitude (Fig. 8).

Figure 5. Relationship between blue duck body mass and structural size.

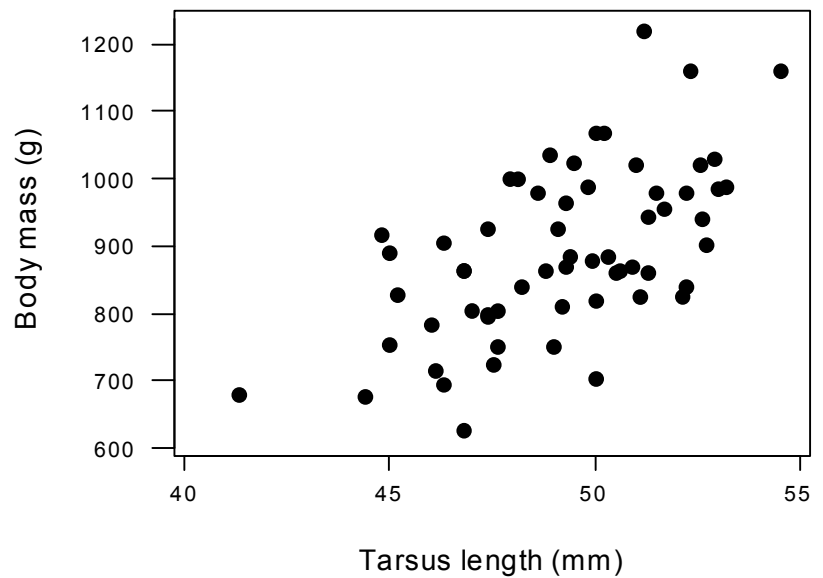


TABLE 5. REML ANALYSIS OF BODY CONDITION (MEASURED AS THE RESIDUAL OF LOGMASS-LOGTARSUS RELATIONSHIP).

	WALD χ^2	DF	P	PREDICTED MEANS
Random effects included				
RIVER				
Fixed effects included				
ISLAND	31.93	1	0.001	North = -0.016, South = +0.057
FLOW	17.14	1	0.001	Natural = -0.004, Regulated = +0.045
SEX	10.33	1	0.001	Male = +0.034, Female = +0.008
STAGE	11.76	2	0.003	Breeding = -0.008, Moulting = +0.036, Post-moulting = +0.034
Covariates excluded:*				
DEE (log kJ)	0.07	1	0.79	
Territory length (log km)	0.21	1	0.65	
Altitude (m a.s.l)	0.39	1	0.53	
Factors excluded:*				
STAGE.SEX	1.56	1	0.46	
SEASON	0.38	1	0.54	
CHANNEL SIZE	0.40	4	0.84	

* Statistics for excluded terms are given at the time of their initial, sequential exclusion; none were significant when re-entered in the final model ($P > 0.1$).

$n = 40$ for DEE, $n = 42$ after DEE excluded, $n = 61$ after Territory length excluded.

Figure 6. Association between river hydrology and blue duck body condition (measured as the residual of the relationship between body mass and tarsus length). Birds from regulated-flow rivers were in significantly better condition than those from unmodified catchments. Data plotted are raw (ANOVA $F_{1,59} = 6.70, P < 0.012$), but a REML analysis, and controlling for STAGE (Fig. 7) and ISLAND and SEX (Table 5), whilst avoiding pseudo-replication due to the repeated measures at single rivers, estimated the significance of this relationship as $P < 0.001$.

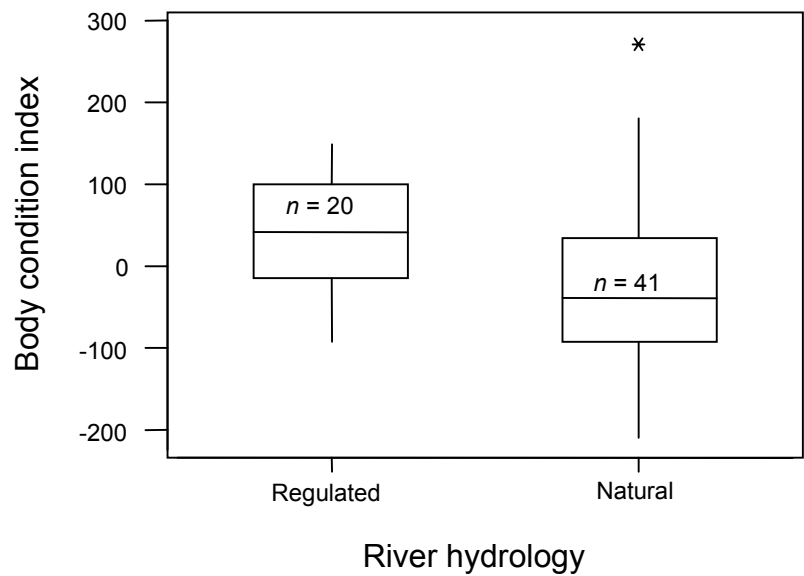


Figure 7. Influence of the yearly cycle on blue duck body condition (measured as the residual of the relationship between body mass and tarsus length). Vertical lines indicate the full range of data, boxes cover the first to third quartile range, and the central line is the median. Sample sizes are indicated. Birds are of relatively low condition during breeding. ANOVA: $F_{2,58} = 7.93, P < 0.001$. Tukey comparisons indicate significant differences between breeding and the other stages, but no evidence for a difference between moult and post-moult stages. These data could be confounded by differences between rivers, but the residuals for the three birds that were caught at two different stages support an effect of stage. REML analysis controlling for SEX, FLOW, and ISLAND and avoiding pseudo-replication due to repeated measures at a single river, estimated the significance of this relationship as $P < 0.003$ (Table 5).

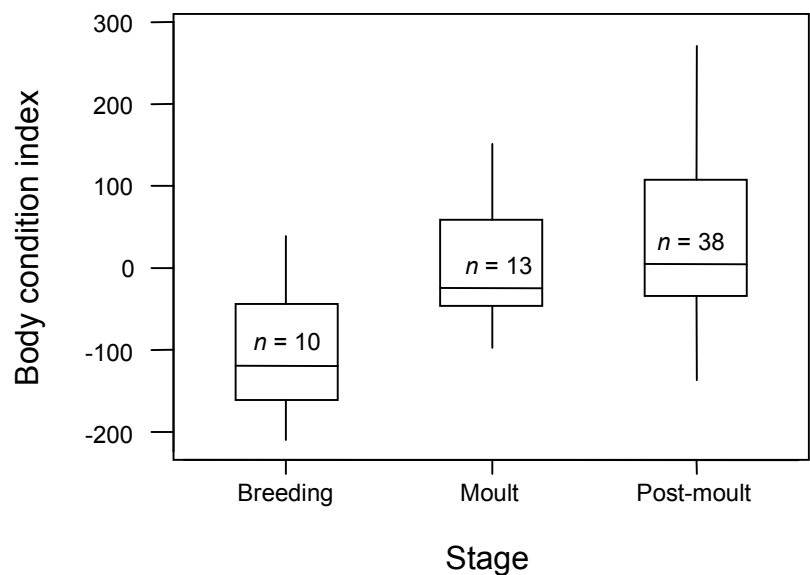
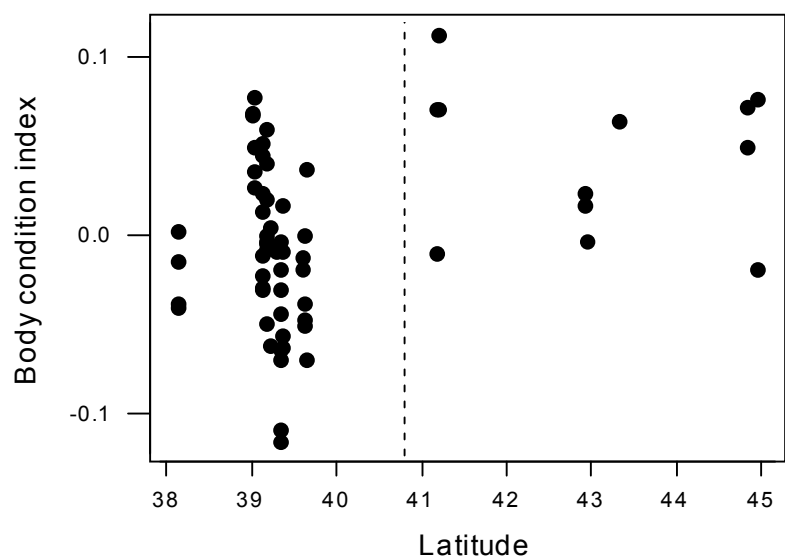


Figure 8. Relation between body condition and latitude in blue ducks. The dotted line approximately indicates the division between North and South Islands. The trend to higher condition in the south is highly significant, either modelled as a linear relationship, or when considered as two distinct populations ($P < 0.005$).



3.5 ENERGY EXPENDITURE IN RELATION TO HABITAT

Principal Components Analysis (PCA) was used to summarise data on habitat structure. PCA axes 1 and 2 were used as covariates in the REML analysis (Table 6). These were calculated separately for the whole data set, and for the set excluding birds from regulated flow catchments. PCA1 was associated with alpine type catchments, whereas PCA2 was perhaps related to catchment modification. Neither PCA axis contributed significantly to variance in DEE (Tables 7, 8).

REML was used to explore variation in energy expenditure between individuals. A primary goal of this research project was to relate DEE to habitat. However, no direct relationship between any measures of habitat quality, habitat structure and energy expenditure (log-transformed DEE) could be detected, with mean breeding density, proportion of birds breeding, juvenile production (/km/year) all being rejected from the model. HABITAT QUALITY rank was also dropped from the model. Similarly neither channel size, slope, body condition, maximum shade temperature, minimum shade temperature, STAGE, ISLAND or FLOW were significant predictors of DEE (Table 7).

Because birds from regulated-flow rivers had, for unknown reasons, different relationships between territory length and altitude, the REML analysis was repeated excluding birds from regulated catchments. For the remaining birds ($n = 30$) body mass ($P < 0.008$), territory length ($P < 0.001$), and altitude ($P < 0.001$) were significant predictors of energy expenditure. Ducks with relatively long territories had higher energy expenditures (Fig. 9, Table 8) ($\text{LogDEE} = 6.68 - 0.522 \log\text{Altitude} + 0.857 \log\text{Territory length}$, $n = 29$, $s = 0.094$, $r^2 = 44.0\%$, $F_{2,27} = 10.62$, $P < 0.001$), but low altitude was associated with high living costs when controlling for the effect of territory length. Nevertheless, the relationship between living costs and territory length was sufficiently strong to be detectable without controlling for other sources of variation (Fig. 10).

TABLE 6. CORRELATION MATRIX OF PRINCIPAL COMPONENTS AXES 1 AND 2 FOR CATCHMENT CHARACTERISTICS OF BLUE DUCK RIVERS, CONDUCTED FOR ALL BIRDS ($n = 41$) AND FOR BIRDS FROM NON-REGULATED RIVERS ONLY ($n = 31$)

CATCHMENT FEATURE	ALL BIRDS		EXCL. REGULATED RIVERS	
	PCA1	PCA2	PCA1	PCA2
Catchment bush	0.49***	0.25	0.49**	0.24
Streamside bush	0.32*	0.53***	0.38*	0.49**
Catchment scrub	-0.40**	0.42**	-0.37*	0.43*
Streamside scrub	-0.45**	-0.02	-0.46**	0.09
Catchment pasture	0.20	-0.69***	0.18	-0.71***
Catchment alpine grassland	-0.50***	-0.02	0.48**	-0.06
Proportion variance	0.50	0.21	0.56	0.25
Eigenvalue	2.98	1.28	3.33	1.50

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

TABLE 7. REML ANALYSIS OF DAILY ENERGY EXPENDITURE (LOG-TRANSFORMED). PCA1 AND PCA2 REFER TO PRINCIPAL COMPONENT AXES RELATING TO CATCHMENT HABITAT CHARACTERISTICS (TABLE 6).

	WALD χ^2	DF	P	COEFFICIENT	SE
Random effects included					
RIVER					
Fixed effects included					
Constant		1		2.772	0.019
LogBody Mass (g)	8.11	1	0.004	0.767	0.030
LogTerritory length (m)	4.67	1	0.031	0.147	0.087
Factors excluded:*					
FLOW	0.24	1	0.63		
STAGE	1.62	1	0.45		
ISLAND	2.45	1	0.12		
HABITAT RANK	2.83	2	0.24		
CHANNEL SIZE	8.41	4	0.08		
Covariates excluded:*					
PCA2	0.00	1	0.97		
Mass change (%)	0.06	1	0.81		
Minimum temperature	0.09	1	0.76		
Body condition	1.27	1	0.26		
PCA1	0.41	1	0.52		
Juveniles produced (/km/yr)	0.50	1	0.48		
Maximum temperature	0.50	1	0.48		
Channel gradient (m/km)	1.10	1	0.29		
Breeding density (log pair/km)	2.90	1	0.09		
Altitude (log m a.s.l.)	2.02	1	0.16		

* Statistics for excluded terms are given at the time of their initial, sequential exclusion, none were significant when re-entered in the final model ($P > 0.1$).

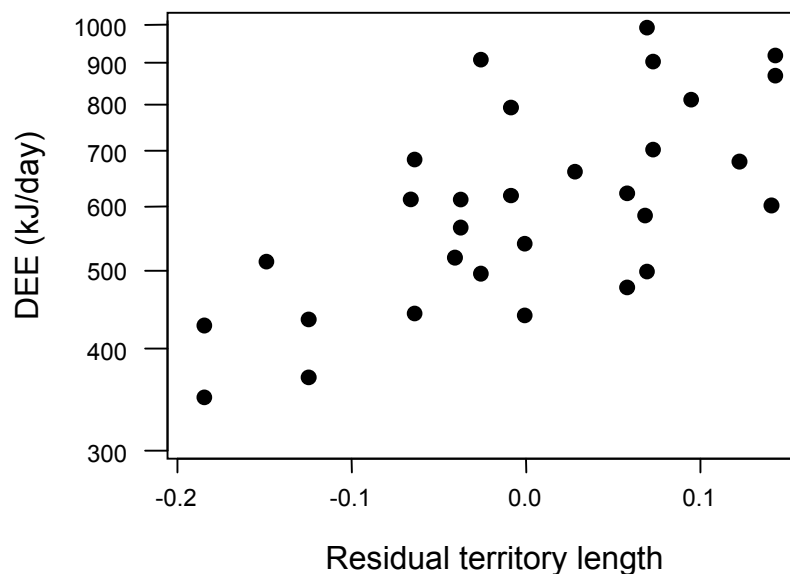


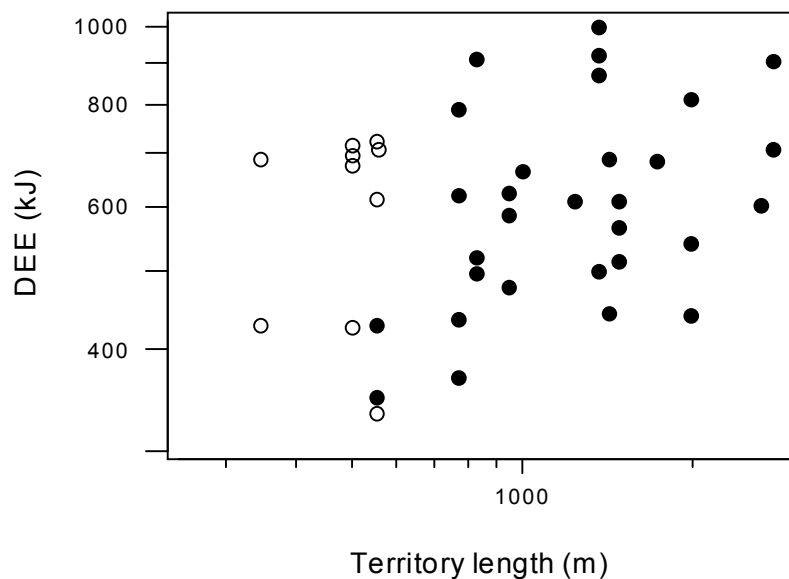
Figure 9. Energy expenditure as a function of variation in territory length after controlling for altitude, using data from non-regulated catchments only. Relatively long territories are associated with high energy expenditure.

TABLE 8. REML ANALYSIS OF DAILY ENERGY EXPENDITURE (LOG-TRANSFORMED) EXCLUDING DATA RELATING TO RIVERS WITH REGULATED FLOW. PCA1 AND PCA2 REFER TO PRINCIPAL COMPONENT AXES RELATING TO CATCHMENT HABITAT CHARACTERISTICS (TABLE 6).

	WALD χ^2	DF	<i>P</i>	COEFFICIENT	SE
Random effects included					
RIVER					
Fixed effects included					
Constant				2.778	0.016
Body Mass (log g)	7.05	1	0.008	0.668	0.252
Territory length (log m)	22.08	1	0.001	0.805	0.171
Altitude (log m a.s.l)	17.70	1	0.001	-0.547	0.130
Factors excluded:*					
HABITAT QUALITY	0.00	2	0.95		
STAGE	0.38	1	0.54		
ISLAND	0.38	1	0.54		
CHANNEL SIZE	1.43	4	0.23		
Covariates excluded:*					
Breeding density (log pair/km)	0.00	1	0.98		
PCA2	0.00	1	0.97		
Body condition	0.01	1	0.92		
Maximum temperature	0.21	1	0.65		
PCA1	0.42	1	0.50		
Minimum temperature	0.39	1	0.53		
Juveniles production (/km/yr)	0.50	1	0.48		
Channel gradient (m/km)	1.62	1	0.20		
Mass change (%)	3.09	1	0.08		

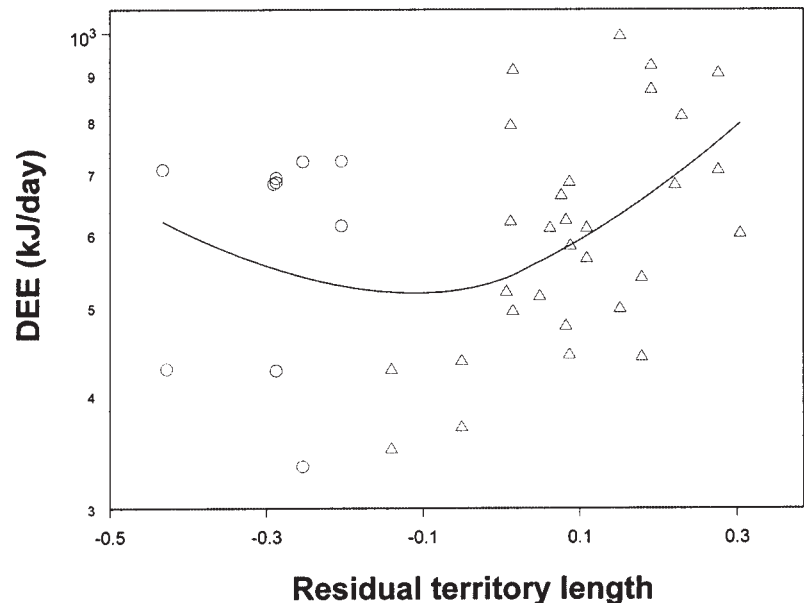
* Statistics for excluded terms are given at the time of their initial, sequential exclusion, none were significant when re-entered in the final model ($P > 0.1$).

Figure 10. Daily energy expenditure (DEE) of blue ducks as a function of their territory length. Natural-flow rivers, filled circles; regulated-flow rivers, open circles. Using simple linear regression, when only natural-flow rivers are considered, the relationship is significantly positive ($P < 0.029$, $n = 30$), but when the regulated-flow rivers are included, this linear relationship is not significant ($P < 0.089$, $n = 40$).



To explore further the relationship between territory characteristics and DEE we fitted a local non-parametric regression (loess) to residual territory length (controlling for altitude) (Fig. 11). Using a locally weighted least squares quadratic function, this procedure fitted a U-shaped relationship, with territories of intermediate length being associated with the lowest expenditures, explaining 18% of the variance in the data. It is meaningless to attach a *P*-value to loess regression.

Figure 11. Local regression (loess) plot of daily energy expenditure (DEE) of blue ducks as a function of territory length, after controlling for altitude. This fit explains 18% of the variance in DEE. Circles show birds from regulated-flow rivers, triangles show birds from natural-flow catchments. Birds holding territories of intermediate lengths have the lowest living costs. The ultra-short territories of birds on regulated-flow rivers seem to entail higher living costs.



3.6 TIME BUDGETS

Behavioural data were collected for 10 pairs of blue ducks, on three regulated rivers (five pairs) and four natural-flow rivers (five pairs) (Table 9). In darkness, using radio-signals alone, it was possible to distinguish 'active' from 'inactive' birds, but not to determine what activity ducks were engaged in: the wavering radio-signal from a preening bird was, in practice, indistinguishable from that from a foraging bird. Night vision equipment was of limited value on open rivers, but was almost useless on tree-covered river sections. As a result, we only present data from daylight time budgets.

Using one-way ANOVA, no effect of gender on any behaviour was detected (all $P > 0.48$) and indeed, pair members maintained close contact at almost all times, and, perhaps as a consequence, had similar time budgets. We therefore used mixed models in REML (Genstat), to avoid pseudo-replication. Both 'pair' and 'river' were included in the random model, so that, when examining other factors, the effects due to individual rivers, and influence between pair members could be accounted for. Controlling for these random model effects, the influence of river FLOW (natural v. regulated flow) and territory length was investigated (Table 10).

When controlling for FLOW, ducks on longer territories rested less ($P < 0.002$), preened less ($P < 0.011$), spent more time engaged in locomotion ($P < 0.001$),

TABLE 9. BEHAVIOURAL TIME BUDGETS FOR 10 PAIRS OF BLUE DUCK ON SEVEN NEW ZEALAND RIVERS.

RIVER	SEX	PERCENTAGE TIME					FORAGING EFFIC.*	OBSERV. TIME (min)
		FEED	MOVE	REST	PREEN	FIGHT		
Whakapapa ^R	M 1	21.4	14.7	50.1	12.5	0.6	0.59	327
	F 1	37.9	17.0	31.9	12.6	0.6	0.69	317
	M 2	10.9	9.2	73.1	5.6	1.2	0.54	464
	F 2	7.6	14.8	73.5	4.3	0.4	0.34	458
Okupu ^R	M	5.8	10.5	79.1	4.7	0.0	0.36	186
	F	14.0	3.7	78.7	3.7	0.0	0.79	136
Tongariro ^R	M 1 [†]	8.9	8.1	65.3	17.8	0.0	0.52	259
	F 1 [†]	11.1	7.6	62.6	18.7	0.0	0.59	198
	M 2	19.2	20.8	54.2	5.8	0.0	0.48	220
	F 2	37.0	18.2	42.9	2.0	0.0	0.67	203
Manganui-a-te-ao ^N	M 1	12.5	10.6	65.2	11.7	0.0	0.54	607
	F 1	4.4	3.5	73.3	10.0	0.0	0.56	607
	M 2	5.8	3.5	84.8	5.8	0.0	0.62	196
	F 2	8.7	10.5	65.8	15.0	0.0	0.45	191
Apia ^N	M	9.2	33.9	49.2	7.7	0.0	0.21	249
	F	14.3	20.6	54.0	10.8	0.0	0.41	225
Flora ^N	M	45.9	9.0	43.6	2.3	0.0	0.84	233
	F	44.4	6.7	43.7	5.2	0.0	0.87	235
Edwards ^N	M	39.6	15.2	40.2	5.0	0.0	0.72	186
	F	32.3	20.8	37.0	9.8	0.0	0.61	192
Mean/Total		19.5	13.0	58.4	8.5	0.1	0.57	5691

* Calculated as feed%/(feed% + move%).

† About 70% of observations by Nancy Staus and James Fraser.

^R Regulated-flow river, ^N natural-flow river.

and tended to spend more time foraging ($P < 0.081$). Similarly, when accounting for the effect of territory length, birds on natural-flow rivers rested more ($P < 0.001$), preened more ($P < 0.001$) and spent more time on locomotion ($P < 0.017$). Foraging time did not differ between natural and regulated rivers ($P < 0.24$). We assumed the proportion of time spent feeding in relation to the proportion spent moving (i.e. feed/(feed + locomotion)) would serve as an estimate of foraging efficiency. This measure did not vary with territory length ($P < 0.97$) or with FLOW ($P < 0.92$) (Table 10).

4. Discussion

4.1 ENERGY EXPENDITURE AND TERRITORY SIZE

Our study confirms expectations regarding the positive relationship between body mass and energy expenditure. Blue duck energy expenditure was strongly coupled to features of the environment, but not in a simple way. Although DEE did not vary directly with altitude, except when regulated-flow rivers were

TABLE 10. REML ANALYSIS OF THE BEHAVIOURAL DATA SHOWN IN TABLE 9. DATA WERE ARCSINE-SQUARE-ROOT TRANSFORMED.

	WALD χ^2	DF	P	COEFFICIENT/ PREDICTED MEANS	SE
Foraging					
Random effects					
RIVER+PAIR					
Fixed effects					
FLOW	1.38	1	0.240	NS	-
LogTerritory length	3.04	1	0.081	0.6009	0.349
Constant				0.415	0.112
Locomotion					
Random effects					
RIVER+PAIR					
Fixed effects					
FLOW	5.73	1	0.017	Nat = 0.194, Reg = 0.470*	0.115
LogTerritory length	11.15	1	0.001	0.627	0.188
Constant				0.332	0.069
Foraging efficiency					
Random effects					
RIVER+PAIR					
Fixed effects					
FLOW	0.01	1	0.921	NS	-
LogTerritory length	0.00	1	0.971	NS	-
Constant				NS	-
Rest					
Random effects					
RIVER+PAIR					
Fixed effects					
FLOW	16.66	1	0.001	Nat = 0.896, Reg = 0.659*	0.058
LogTerritory length	9.22	1	0.002	-0.508	0.167
Constant				0.777	0.026
Preen					
Random effects					
RIVER+PAIR					
Fixed effects					
FLOW	10.68	1	0.001	Nat = 0.323, Reg = 0.240*	0.025
LogTerritory length	6.54	1	0.011	-0.246	0.096
Constant				0.281	0.007

* Predicted means shown are arcsine-square-root transformations, back-transformed means are:
Locomotion: Natural = 3.77%, Regulated = 21.95%; Rest: Natural = 71.92%, Regulated = 42.11%;
Preen: Natural = 10.77%, Regulated = 5.75%.

excluded, it was positively related to territory length, which was itself altitude-dependent. Birds with relatively long territories at any altitude had high DEEs. Alternatively, birds living at relatively high altitudes for their territory size had low energy expenditures. Considering birds from natural-flow rivers alone, 44% of the variance in DEE could be attributed to this combination of territory length and altitude (Fig. 9).

Using what are now known to be *over*-estimates of blue duck energy expenditure ($3 \times \text{BMR} = 818 \text{ kJ}$ for 717 g birds), Veltman et al. (1991) calculated that on one river, the Manganui-a-te-ao, adults required the chironomid larvae present in 1.24 m^2 of river bed to meet their daily energy requirements. By replacing our mean measure DEE for blue ducks (617.4 kJ), the area apparently required is reduced to 0.94 m^2 . Arguing that chironomid recolonisation rates are high (see Williams & Hynes 1976), and that areas of the duck territories were about $10\,000 \text{ m}^2$, Veltman et al. (1991) concluded that territories were not defended as a food resource.

There are a number of problems with this conclusion. In the first place, the total area of a territory does not reflect the total usable area: a detailed radio-tracking study (Johnstone 1994) of the European dipper *Cinclus cinclus* (an ecologically similar bird) showed that foraging occurred on disjunct lengths of river within a substantially unexploited total territory. Previous work (Williams 1991, Collier & Wakelin 1996), together with observations during this study (J.D.G. pers. obs.), suggests that blue ducks similarly exploit only parts of their territory. Secondly, as Veltman et al. (1991) acknowledged, territories may be defended as insurance against catastrophic flood events or other short-term declines in food availability. Thirdly, the density of invertebrates present in 2 m^2 may bear little relation to the number available to ducks over a given time period: in addition to reduced prey density following removal, duck foraging may cause local prey disturbance, reducing capture opportunities (e.g. Charnov et al. 1976, Yates et al. 2000). Under such circumstances the 'recovery time' (Davies & Houston 1981) must be known before an economic analysis can be applied. Observations of ducks reveal they do not spend long in small areas, but are constantly moving whilst foraging, suggesting that higher energy gain rates can be achieved by moving from a disturbed to a fresh site. Duck movements while foraging tend to be in a consistent direction, so that they progress from one end of the territory to the other (J.D.G., M.W. pers. obs.). Finally, Collier et al. (1993) showed that presence or absence of blue duck in stretches of river was related to aspects of river morphology and invertebrate assemblages, indicating a connection between food resources and territories.

These points suggest that it is unwise to infer an absence of a resource constraint on territory size based simply on densities of potential food items. Indeed the evidence is consistent with blue ducks being limited by the availability of food resources on their territories.

4.2 EFFECTS OF ALTITUDE

Blue duck are culturally associated with the uplands (Kear 1972), but occur across a range of altitudes, and it is not obvious whether altitude is related to habitat favourability, nor, if it is, whether lower or higher altitudes are the more favourable. Altitude may be linked to food supply, e.g. lower average temperatures associated with higher altitudes depress invertebrate production both directly (Morin et al. 1995, Gresens 1997, Benke 1998), and indirectly through reduced allochthonous nutrient input; an important source of blue duck carbon (Collier & Lyon 1991), whereas the relationship between volume

of extrinsic nutrient input and altitude is likely to be negative although it may be offset by increased primary production in unshaded channels above the tree line (Weigelhofer & Waringer 1994). Thus, resource density *per se* may not be an appropriate measure of the feeding utility of a territory. For example, 'Recovery time' (see above) may itself be related to water temperature, or other river features correlated with altitude. Similarly, high-altitude territories may be more prone to periodic catastrophic declines in prey availability, resulting either from heavy flooding washing a large proportion of food downstream, or from river icing. On the other hand, high-altitude zones may be *less* prone to catastrophic flooding than areas lower in the catchment, where flood-waters gather. Under these circumstances stream order may be more pertinent for recolonisation rates than absolute altitude. Finally, systematic differences in prey assemblages with altitude could influence foraging costs and returns. Although some studies have suggested specific prey preferences in blue duck (Collier *et al.* 1993) similar to that found in the European dipper (Ormerod *et al.* 1985), later work suggests a more opportunistic approach to feeding (Veltman *et al.* 1995).

Our data imply that altitude is related to reduced resource density, since, at least on natural-flow catchments, territory length was closely correlated with altitude (Fig. 4.). There is some evidence that high altitudes reduce habitat-wide breeding success in blue duck in terms of juveniles produced per unit river length (Fig. 3), although breeding pair density was not related to altitude, implying reduced individual fitness (or else higher juvenile survival rates) at altitude. If territories were indeed economically determined, then larger rivers might be expected to support shorter territories (of similar area), yet ranked channel size seemed to explain little variation in territory length. Since blue duck foraging seems to occur principally at the river margins (Veltman & Williams 1990; Collier & Wakelin 1996; J.D.G. pers. obs.), length could be a better estimate of territory resources than area. Previous studies have reported similar negative correlations between linear breeding density and altitude for the European dipper (Newton 1989; Logie *et al.* 1996). This relationship between altitude and territory length can be rationalised within the traditional economic model of territories (Gass *et al.* 1976; Kodric-Brown & Brown 1978, Davies & Houston 1984; Vickery 1991): reduced resource density at high altitudes requiring the maintenance of larger territories with reduced returns from foraging per unit time, and potentially elevated defence costs. Further reduction in resource density could raise costs to such an extent that territoriality is no longer economically viable. The positive relationship between territory length and DEE amongst birds on natural flow rivers seems to confirm this interpretation. However, when controlling for territory length, the partial correlation between living costs and altitude was *negative*.

4.3 TERRITORY ECONOMICS

One way of interpreting the opposite direction of relationships of territory length and territory altitude (when controlling in each case for the effects of the other) with DEE is to consider the two component living costs of territorial economics, foraging and defence, separately. Traditional defence cost models

consider approximately circular territories in which costs are proportional to area, because larger territories have greater intrusion rates, and defenders must travel further to patrol borders or evict intruders (Davies & Houston 1984). Blue duck territories, however, being linear, perhaps do not fit this model. Our results could make sense if, whilst resource density decreased with altitude and so led to longer territories and increased *foraging* costs, the longer territories themselves led to reduced territorial *defence* costs. This could be the case if meetings with neighbours at mutual boundaries in the course of territory exploitation form a significant component of defence costs, since birds on longer territories would be expected to spend proportionately less time at territory boundaries during the course of foraging routines. Furthermore, the area of adjacent habitat through which intrusions can occur is independent of territory length. Essentially every territory has two intrusion points with the exception of two special cases: territories at either the upper or lower extreme of usable habitat (one intrusion point); and those centred on a confluence of two channels (three intrusion points). So whilst the number of neighbouring intruders entering a territory could be independent of territory length, longer territories would give intruders lower chances of being detected. Thus there are two mechanisms which could account for lower territorial defence costs on longer territories. It is important to note that this interpretation applies to defence of an established territory, not to the act of establishing one. In this latter case, costs are likely to be positively related to territory length, because of the necessity of frequent visits to both 'borders.' We assume that all ducks in the present study were defending established territories.

We present a graphical model of territory economics in relation to territory length, by considering three distinct costs: foraging costs, mutual boundary or neighbour disputes, and disputes with intruders on the territory (which may or may not be neighbours) (Fig. 12). We assume that neighbours and focal birds have territories of the same length (dependent on habitat-wide resource density). We further assume that ducks spend equal time in all sections of their territory. We use simple probability to show how neighbourhood structure could influence living costs, and calculate the likelihood of residents and neighbours being in adjacent sections (i.e. by their mutual boundary), which we use as a proximate measure of likely neighbour-defence costs. The notional lengths of the sections into which territories are divided represent the range at which other ducks can be detected. These are independent of territory length. We assume, too, that number of intrusions is independent of territory length, since all territories are considered to have only two entrance points. We model the detection of intruders in proportion to the likelihood of intruder and resident being within this detection range, based on random positioning of both resident and intruder. In this way we generate length-related costs for territory defence against intruders and neighbours. Both increase exponentially as territory size contracts (i.e. as detection range increases relative to territory length). At the same time we assume that foraging costs increase with territory length, because length reflects resource density, and so the time taken to meet 'standard' energy requirements increases. This relationship is non-linear, because the additional energy spent on meeting the 'standard' living costs on longer territories itself requires an additional amount of foraging to balance its marginal cost. Furthermore, if foraging patches become more widely spaced in

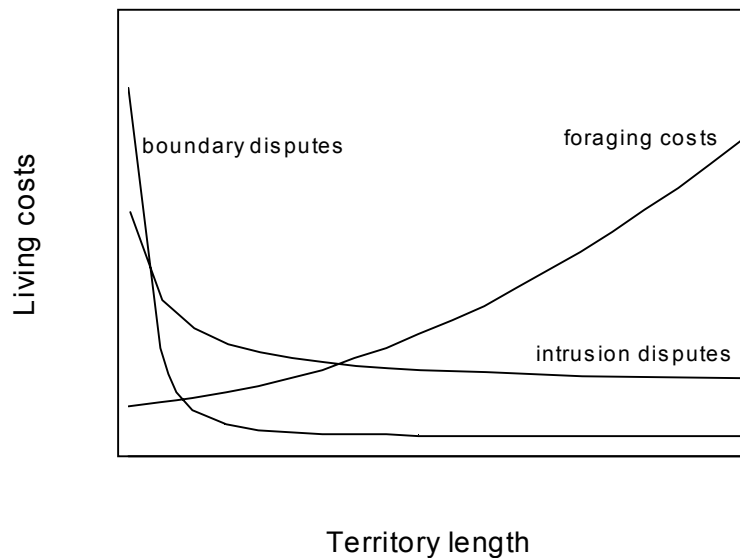


Figure 12. Model of territory living costs for blue ducks. Foraging costs rise as an accelerating function of territory length. Since territory length is assumed to reflect resource density, costs accelerate because longer territories require more non-productive locomotion between foraging patches, in turn requiring more time (and energy) to be spent foraging to meet increased energy demands. Boundary disputes vary with territory length as a decelerating function relating to the probability of both residents and neighbours being within visual range of a mutual boundary. Intrusion disputes vary as a shallower decelerating function, because whilst probability of neighbours being within detection range depends on both neighbouring and focal territory lengths, intrusions are assumed to be independent of habitat-wide territory lengths. This is because all territories have only two access points. Intruder detection is based on the probability of intruders being within detection range of residents. We are unable to estimate the relative costs of boundary disputes, intrusion disputes and foraging.

longer territories, foraging costs must themselves accelerate with territory length. Our model predicts that living costs are a U-shaped function of territory length (Fig. 12).

All the territories on regulated rivers were short, and although amongst natural rivers short territories were associated with low living costs, there was no tendency towards low expenditure amongst birds on regulated-flow rivers (Fig. 10). The inclusion of regulated-flow rivers in the linear analysis of the relationship between territory length and DEE changes a significant relationship ($n = 30, P < 0.029$) into a non-significant one ($n = 40, P < 0.089$). The apparent termination in the decline in living costs with territory length at the range represented by regulated flow rivers could reflect the increasing cost of defence in short territories. Local regression of energy expenditure on residual territory length generated a U-shaped curve (Fig. 11), consistent with the predictions of our model (Fig. 12). Unfortunately we need additional information on river morphology, detection range, and the relative costs of intruder disputes and boundary disputes to explore the predictive power of the model further. Furthermore, it is worth noting that the data points from the regulated-flow rivers appear to fall into two distinct groups of high and low expenditures. Possibly the low expenditure group represent non-territorial birds, or those without mutual boundaries, or simply those where boundaries are rarely disputed due to long-term establishment. Such differences possibly contribute to considerable 'noise' in the relationship between population density and defence costs.

Our model assumes that all birds have two sets of neighbours. However, low resource availability at altitude could reduce local population density, allowing expansion of territories into unoccupied areas. This could account for a further decline in living costs with altitude when controlling for territory size, because it would involve the removal of the defence-related constraints on territory length at high altitudes. This would permit the existence of longer territories at altitude than predicted from resource density alone. Birds without neighbours could then allow stream benthos a longer recovery time, and so perhaps reduce living costs by increasing net energy gain rates. Data for the catchments do not encourage this interpretation, however, because despite birds occupying longer territories at altitude, there was no evidence for a decline in overall breeding pair density with altitude.

4.4 BEHAVIOUR

Our time budgets suffered from several weaknesses. In the first place, an unknown, but possibly large, error may result from the relatively short time budgets we were able to collect. Blue duck behaviour tended to be episodic, with bouts of resting interspersed with foraging, and the duration of these bouts relative to the duration of our time budgets was sufficient to generate significant noise. Furthermore, blue duck behaviour is not likely to be distributed evenly throughout the day, and we were not able to control for diurnal effects. Nocturnal radio-tracking suggested that night-time activity patterns differed markedly between rivers, but we could not reliably determine in what way. An additional problem is that we were unable to attribute a functional goal to some behaviours. For example, locomotion may have been chiefly related to foraging for some birds/rivers, but to territorial defence for others.

Nevertheless, the behaviour of ducks could be related to territory length: both time spent in locomotion, and foraging time increased with territory length (although the latter, at $P < 0.081$ did not quite meet the 0.05 significance criterion). If we assume that movements are related to foraging, these data are consistent with our model of territory economics (Fig. 12). Foraging efficiency did not appear to be related to territory size, however, suggesting that the increased foraging time on longer territories related to lower resource density overall, rather than to increasing distances between patches. It is possible that a trend towards a greater territorial defence component (or decreasing foraging component) in locomotion with decreasing territory length exists, tending to obscure a negative effect of territory length on the measure of foraging efficiency used here. The scarcity of recorded territorial behaviour does not encourage the view that territorial defence costs will be strongly correlated with territory size. However, all the recorded fighting by ducks was on short territories (Table 9), and if territorial defence is energy-intensive it might occupy relatively little time but still influence energy expenditure. Incidental observations suggested that our time budgets may have underestimated the proportion of time devoted to defence, and that territorial contests, involving long flights as well as fights, could be energetically costly.

Behaviour in relation to FLOW is rather more difficult to understand. The REML models (Table 10) indicate that flow regulation tended to increase locomotion, reduce resting and preening, whilst having no impact on foraging or foraging efficiency. Unless movements amongst these birds are associated with territory defence, these data do not accord with our model of territory economics, because we do not expect an effect of FLOW over and above territory length. These data imply that flow regulation itself is associated with increased locomotion and/or (since behavioural proportions are not independent of each other) decreased resting/preening. Conceivably flow regulation has led to increased fragmentation of foraging patches. Alternatively the types of river suitable for water extraction may have had these characteristics before extraction began.

4.5 INDIVIDUAL QUALITY AND TERRITORY SIZE

Although it is possible to explain DEE as a function of territory size and altitude, there is no evidence for the direction of causality. Territories might be longer to meet the high living costs imposed by the general nature of the habitat, or living costs might be higher because territories are longer. If territory length reflected male aggressiveness (e.g. Moss et al. 1994, 1995), we might attribute high energy expenditure to high levels of circulating steroids in males, which are likely to elevate both basal metabolism and field metabolic rate (Högstad 1987; Bryant & Newton 1994; Marler et al. 1995). Accordingly, we might anticipate that the relationship between DEE and territory length and altitude was confined to males. In practice female DEE showed slightly stronger coupling, but there was little difference between the sexes. This situation could still arise if high-cost aggressive males tended to pair with similarly high-cost females, or if aggressiveness in males entailed similar high-cost behaviour in females (see Eldridge 1986; Williams 1991). There was some evidence that male and female DEE were associated, because, after accounting for the effects of sex, pair members tended to have more similar energy expenditures than birds from other pairs ($P < 0.042$). However, where DEE measures were obtained for both pair members, the birds were invariably caught and recaptured together, so this result is confounded by many factors, including territory, river, and weather conditions, and so may reflect only the consensus of common local factors.

4.6 BODY CONDITION

Body condition of blue ducks varied in time and space: southern birds were in 'better condition' (= 'fatter,' although reserves may be of protein and/or fat), and breeding birds in lower condition (= 'thinner') than moulting or post/pre-moult birds. Females were thinner than males, and birds from regulated-flow catchments were fatter than those from natural catchments. Interpretation of body condition is not straightforward (Witter & Cuthill 1993; Gosler 1996). Reserves can be viewed as an indicator of past events, as an investment in future reproduction, or as an insurance against starvation. In the first case 'good condition' implies good habitat, but in the last it implies variable or risky

habitat. In avian research, the focus on the winter reserves of passerines (Houston & McNamara 1993; Godfrey & Bryant 2000) has tended to stress the costs of being fat, by modelling reserves as a trade-off between the twin risks of starvation and predation. Under such circumstances, being in 'good condition' implies either a higher risk of starvation, or a lower risk of predation (Houston & McNamara 1993) with, for example, dominant birds carrying fewer reserves than subdominants because of the former's surety of access to feeding sites (Ekman & Lilliendahl 1993). However, where predation risk is low, and interspecific competition is more likely to regulate population size (as is probably the case for the blue duck, at least in evolutionary time), the costs of carrying fat may be relatively low (particularly for birds that fly only rarely). Under these circumstances, reserves may increase with food availability over a wide range (Lima 1986; Lovvorn 1994; Godfrey 1997), so that body condition may reflect good conditions rather than risk.

Blue duck condition varied with gender, latitude, stage of the yearly cycle, and catchment hydrology, but was not related to altitude, territory length, or DEE (Table 5). Only the relationship with breeding stage offers a way to resolving the function of body reserves in blue duck. Breeding birds were lighter than moulting and post/pre-moult individuals. This could be interpreted as either an indication of the impact of increased vigilance and hence reduced foraging during chick-rearing, or simply as a result of breeding effort. Equally it might reflect breeding being timed when resources were common, or more predictable, and risk of starvation was low. Only two studies seem to have analysed temporal variation in larval invertebrate abundance on blue duck rivers, and both found the lowest numbers during January, with an increase in numbers through the winter (Veltman et al. 1991, Veltman et al. 1995), a pattern common in temperate running waters. Though limited, these data tend to suggest that body condition reflects food availability rather than risk, because condition seems to increase rather than decrease with resource density. However, very little is known about short-term variance in blue duck feeding opportunities (Collier & Wakelin 1991; Veltman et al. 1995). It might be assumed that flooding causes a hiatus in feeding, although during the course of this study most birds gained condition during spates (J.D.G. unpubl. data), possibly feeding profitably on displaced invertebrates washed up on riverbanks.

Some evidence (Collier et al. 1993) suggests a lower resource density in South Island rivers, although we found the South Island birds to be in better condition. Since this appeared to be a distinct rather than clinal change between islands (Fig. 8), and since blue duck dispersal is low (Williams 1991; Triggs et al. 1992), this could reflect a genetic rather than an ecological effect. A similar explanation probably accounts for the apparent lower condition of females.

If body condition covaries with resource availability, our data suggest that blue ducks living on regulated-flow rivers can acquire food easily. This view is supported by the shortness of territories defended on regulated rivers, implying high resource density. Alternatively, if short territories are associated with an increase in territorial disputes, increased body mass might be an adaptive response conferring advantage in aggressive encounters. If this were the case, then we anticipate that the increased 'condition' in these birds would arise

from increased protein reserves (muscle tissue) rather than increased fat storage.

4.7 FLOW REGULATION

The impact on blue ducks of water extraction for hydro-electricity has received considerable interest within the Togariro/Taupo Conservancy of the Department of Conservation, and the view that flow regulation is deleterious to duck populations is widely held. Evidence for this appears equivocal. The chief difficulties are firstly that pre-flow regulation data on blue ducks are scarce, and secondly that *a posteriori* comparisons of natural and regulated rivers are confounded by rivers not having been randomly selected for flow regulation.

Despite this interest, and despite many studies involving invertebrate sampling on blue duck rivers (Collier 1991, 1993; Collier & Wakelin 1991; Collier et al. 1993, 1995; Veltman et al. 1991, 1995), no comparison of invertebrate populations between blue duck rivers with regulated and natural flow seems to have been made. River impoundment is generally found to reduce macro-invertebrate diversity and increase biomass and productivity (Armitage 1978, Petts 1984, Weisburg et al. 1990, Raddum & Fjellheim 1993, Petts et al. 1993). However, different types of regulated flow regimes can lead to markedly different effects (Fjellheim et al. 1993), and extremes of flow manipulation can cause dramatic reduction of both diversity and density (Trotzky & Gregory 1974, Petts 1984). Furthermore, effects of flow regulation on invertebrates can vary significantly with time elapsed since the flow regulation began (Greenwood et al. 1999). Straightforward predictions concerning the effects of flow regulation on food supply for blue ducks are therefore not possible. Every river may need individual examination, although the clustering of territory lengths on regulated rivers (Fig. 4) implies differences within the group of regulated rivers are trivial compared to differences between regulated and natural catchments.

Distinct extraction sites with natural flow upstream and regulated flow downstream (e.g. the Whakapapa River intake structure) allow an immediate experiment of the effect of flow regulation on food supply. Sampling invertebrates at various points above and below the structures would give a broad view of the impact of flow regulation, whilst short-term effects of variation in flow downstream of intake structures should lead to further insight into the connection between regulation and the structure of invertebrate populations. The effect of flow regulation on the relationship between mean flow volumes and channel morphology could influence invertebrate availability to ducks in a way not easily measured by invertebrate sampling. For example, the large channels eroded by formerly greater volumes of water may cause the reduced post-modification flow to form broader, shallower rivers that might be expected to suit blue duck foraging preferences for shallow water (Collier & Wakelin 1996).

In the absence of data on food supply we cannot comment firmly on the cause of higher body condition in regulated flow rivers, but there seems to be no evidence to support the view that high levels of reserves reflect high risk of

starvation. In fact, the evidence available suggests that regulated flow rivers of central North Island represent high-quality habitat for blue ducks. Data available for three regulated-flow rivers show that blue duck occur at a higher overall density, require shorter territories, yet breed at similar rates, and have similar individual breeding success, so that production of juveniles per unit length is greater than for other rivers. While our measures of energy expenditure suggest that this entails higher than expected energy expenditure, perhaps related to increased territory defence costs, there is no available information to explore how this might relate to survival.

4.8 ADULT SURVIVAL

The nine-year study by Williams (1991) on the Manganui-a-te-ao River, central North Island provides probably the only reliable estimate of adult blue duck survival, where annual survival of territory holders was 0.86. Two other, shorter, studies give estimates of adult blue duck survival: 0.75 on the Flora Stream (Kahurangi National Park, Shaw 1996); and 0.85 on the Apias River, and 0.82 on the neighbouring Makaroro River (Ruahine Range, J.Adams, unpublished data). These data do not suggest wide variation in survival rates, but no estimates are available, at the time of writing, for regulated-flow rivers.

Under conditions in which habitat-wide breeding failure can occur, e.g. in El Niño years (Williams 1991), adult survival could be the crucial determinant of habitat quality, if this is defined as the likelihood of sustaining a population into the future. Since increased energy expenditure has been linked to reduced survival or delayed breeding in other birds (Daan et al. 1996; Deerenberg & Overkamp 1999), we might anticipate that highest survival would be associated with low living costs for ducks, and we expect living costs to be lowest at intermediate length territories (Figs 11, 12). The long territories associated with high altitudes, and the very short territories on regulated flow rivers may both lead to increased living costs, and so to reduced survival. As a multiple of basal metabolism, blue duck living costs do not approach the level at which survival costs are typically expected to occur (Bryant & Tatner 1991). Whether the 4.5BMR ceiling (Drent & Daan 1980) developed for Northern Hemisphere birds is appropriate to New Zealand is, however, not clear.

4.9 STUDY SCOPE

Only one natural-flow river has similar population density and breeding success to the regulated flow rivers of central North Island: the nearby, but lower-lying, Manganui-a-te-ao. Of the 13 refereed papers investigating blue ducks cited in this report, eight focus exclusively on the Manganui-a-te-ao, three on the Manganui-a-te-ao and other rivers, and only two (one of which describes blue duck distribution in South Island) do not include this river. Concentration on a single type of blue duck habitat has provided much useful detail, but has perhaps tended to obscure broader trends. The breadth of the present study has

enabled general patterns of blue duck ecology, not previously explored, to be revealed.

A weakness of this broader approach, however, is that it requires the bringing together of population data from disparate sources, sometimes collected by different methodologies and over different years. Although there are inevitable within-site and between-site errors as a result, we believe that our comparative approach is a useful basis for understanding variation in blue duck breeding and survival, and advancing knowledge of the bird's survival.

5. Management implications

Our primary aim, to develop a framework for identifying blue duck populations of particular conservation significance, was not achieved. Free-living energy expenditure alone cannot provide sufficient information to determine habitat quality for these birds. This is in part because variation in energy expenditure is high, requiring large sample-sizes to determine significant differences, and in part because the factors involved in energy use by these birds was complex.

However, this study has identified certain measures that warrant further investigation. Territory length has emerged as a crucial factor involved in the behaviour and energy expenditure of blue ducks, and the evidence suggests that blue ducks may be strictly limited by food availability. This implies that resources determine habitat quality, and suggests that predation may be less important for blue duck population viability than for some other endangered birds in New Zealand.

Energy measures suggest possible negative impacts on survival for birds of both very long and very short territories. Long territories were associated with high altitude, (itself related to reduced juvenile production (Fig. 3)), and so probably represent marginal habitat for blue duck. On the other hand, the very short territories found on regulated-flow rivers, though possibly representing a cost to adult survival, are associated with the highest productivity. Unless these rivers confer particularly high variation in breeding success, it is unlikely that any slight negative impact on adult survival would offset the higher juvenile production rates.

Nevertheless, the implication of the foregoing is that rivers with intermediate-length territories (in this study, the Takaputahi and Manganui-a-te-ao) may support the most robust populations, and serve as 'sources' rather than 'sinks' for the population as a whole. Understanding the determining factors of territory size in blue ducks, perhaps by more comprehensive behavioural observations than those reported here, and by detailed analysis of food supply across a range of different territories and rivers, offers a way forward in the conservation management of this species. Although a great deal of effort would be required to establish adult survival in different habitats, and to relate that to territory size, breeding success and body condition, it could reveal trends important to the understanding of habitat quality in these birds.

6. Acknowledgements

The study was funded by the Department of Conservation as part of research investigation 2419. A grant from the Natural Environment Research Council (UK) to D.M.B. allowed analysis of doubly labelled water samples.

Duck-catching is a team effort, especially on big rivers. J.D.G. acknowledges the many keen and able field-workers who helped catch ducks, or at least helped make not catching ducks bearable. The cast, in order of appearance, was Murray Williams, J.D.G., Miles, Bob, Norm, Peter, Dean Caskey, Wayne Hutchinson, Brian, Duncan Cunningham, Kerry Oates, John Adams, Peter Abbot, Dyksey, Harry Keys, Cam Speedy, Peter Morton, Nancy Staus, James Fraser, Ross, Tim Shaw, Kirsty, Peter Quillan, Graham, Nikki, Kerry, Martin, Phil, Campbell, Anna, Sheryll, Mike, Janie, Dean Turner, Wayne Reid, Christian Chester, Murray Willans, Jane Maxwell, Max Smart, Lynn Adams, Chris, Rob McCallum, and about half a dozen other people whose contributions were of great value. Other DOC staff offered useful advice, notably Ralph Powlesland, Clare Veltman, and Murray Douglas. Nancy Staus and James Fraser helped collect time budgets on the Tongariro River. Tim Shaw helped crystallise ideas on territory defence.

In Scotland, discussions with Ian Stevenson and Karen Spencer have helped focus thinking, and Ian also helped with understanding Genstat's eccentric REML output. J.D.G. and Jim Weir carried out the stable isotope analysis at the Scottish Universities Research and Reactor Centre. We thank Jim for his tireless efforts, and Susan Waldron at the National Environment Research Council Life Sciences facility at SURRC, East Kilbride, for the provision of facilities.

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