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Time–activity budgets and energetics of Dipper *Cinclus cinclus* are dictated by temporal variability of river flow

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Abstract

The white-throated Dipper (*Cinclus cinclus*) is unique among passerine birds by its reliance on diving to achieve energy gain in fast-flowing waters. Consequently, it should have evolved behavioural adaptations allowing responding directly to runoff patterns (one of the assumptions of the Natural Flow Regime Paradigm—NRFP). In this study (October 1998–August 2001), we investigated how behavioural and energy use strategies in Dippers might vary under the natural flow regime of snowmelt-dominated streams in The Pyrénées (France) where natural flow regime is highly seasonal and predictable. We recorded time spent in each of 5 behavioural activities of ringed birds to estimate time–activity budgets and derive time–energy budgets enabling the modelling of daily energy expenditure (DEE). Annual pattern in 'foraging' and 'resting' matched perfectly the annual pattern of the natural regime flow and there was a subtle relationship between water stage and time spent 'diving' the later increasing with rising discharge up to a point where it fell back. Thus, time–activity budgets meet the main prediction of the NRFP. For males and females Dippers, estimates of feeding rates (ratio E_{obs}/E_{req}=*observed* rate of energy gain / *required* foraging rate) and energy stress (M=DEE / Basal Metabolic Rate) also partly matched the NFRP. Maximum value for the ratio E_{obs}/E_{req} was registered in May whilst M peaked in spring. These ratios indicated that Pyrenean Dippers could face high energy stress during winter but paradoxically none during high snowmelt spates when food is expected to be difficult to obtain in the channel and when individual birds were observed spending ca 75% of the day 'resting'. Annual pattern in DEE did not match the NFRP ; two phases were clearly identified, the first between January to June (with oscillating values 240–280 kJ d^{-1} ind^{-1}) and the second between July and December (200–220 kJ d^{-1} ind^{-1}). As total energy expenditure was higher during the most constraining season or life cycle, we suggest that energy management by Dippers in Pyrenean mountain streams may fit the 'peak total demand' hypothesis. At this step of the study, it is not possible to tell whether Dippers use an 'energy-minimisation' or an 'energy-maximisation' strategy.

Keywords: River bird; Natural flow regime paradigm; Energy stress; Feeding rates; Adaptive energetics; 'peak total demand' hypothesis; FMR/BMR ratio; E_{obs}/E_{req} ratio

1. Introduction

The natural flow regime paradigm (NRFP) has become a fundamental part of the management and basic biological study of running water ecosystems (Poff et al., 1997). It postulates that "the structure and function of a riverine ecosystem, and the adaptations of its constituent riparian and aquatic species, are dictated by the pattern of temporal variation in river flows" (Lytle and Poff, 2004). Organisms have adaptations for surviving or exploiting historic cycles of natural flood and drought (the so-called natural flow regime, NFR). Flow regime adaptations range from behaviours that result in the avoidance of individual floods or droughts, to life-history strategies that are synchronized with long-term flow patterns (Lytle and Poff, 2004). If it is true for all organisms, specialist river birds (*sensu* Buckton and Ormerod, 2002) should have developed such adaptations that should be revealed in activity pattern and energy use. As there are good subterranean mammal models (such as the genus *Ctenomys*) to evaluate the hypotheses about

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cost of burrowing and thermal stress (Luna and Antinuchi, 2007), aquatic bird models (such as Penguins, Guillemots and Cormorants) to test hypotheses on diving physiology, optimal patch uses and optimal diving for example in oceanic environments (Ponganis and Kooyman, 2000; Grémillet et al., 2001; Niizuma et al., 2007), one should find good model to test the energy-distribution hypotheses in fast-flowing streams.

Among specialist river birds, Dippers (genus *Cinclus* in the family Cinclidae) are such candidate models. They are widespread (Voelker, 2002) and are unique as they are the only passerines adapted to make use of aquatic habitats by swimming and diving. They usually require fast-flowing and well-oxygenated waters where stony beds especially offer abundant invertebrate preys such as caddis-fly larvae (Trichoptera), stoneflies (Plecoptera), mayfly nymphs (Ephemeroptera) but also calcium-rich molluscs, crustacean or small fishes during the pre-breeding stage (Ormerod and Tyler, 2005). They are thus considered good indicators of changes in water quality (Ormerod and Tyler, 1993). Among the five species known in the world (Voelker, 2002;Lauga et al., 2005), the White-throated Dipper (*Cinclus cinclus*) has the widest distribution occurring in Europe, North Africa and Asia. Its ecology has been extensively considered (Spitznagel, 1985; Tyler and Ormerod, 1994) and researchers still exploit the ease with which it can be studied to develop both influential and novel research lines (Ormerod and Tyler, 2005). In particular, the seminal studies on activity pattern and energy use by David Bryant et al. (Bryant, Hails and Prys-Jones, 1985; Bryant and Tatner, 1988; Bryant and Newton, 1994; Bryant and Newton, 1996; Brown and Bryant, 1996) are of considerable importance. Since that time, the use of time–activity budgets (TAB) to derive time–energy budgets (TEB) has proved to be a convenient approach to assess a bird's use of time and energy expenditure (Bryant et al., 1985; Goldstein, 1988). Total Daily Energy Expenditure (DEE) can then be obtained from the sum of costs, as multiples of metabolic rates, of different behavioural activities (Goldstein, 1988; Bryant and Tatner, 1988; Nagy, 1989). Because energetic costs vary according to time spent in different behavioural activities, it is straightforward to use TAB to evaluate the effects of changes in feeding strategies and resting on overall energetic budgets. In the case of the White-throated Dipper, given its dependence upon diving to acquire food and thus energy, it is likely that the shaping environmental conditions (e.g. velocity, depth, turbidity…) and its variation across the year that make stream an unique ecosystem will have a considerable impact on the annual energetics of the species. For those reasons, this species is an interesting organism to test some of the assumptions of the NFRP.

Although two specific studies described annual pattern of TAB and TEB (in Scotland, Bryant and Tatner, 1988 and in Wales, O'Halloran et al., 1990), none tried to relate them to the local pattern of annual variation in river flows. Yet, no study has ever been published to describe TAB and TEB in the context of highly demanding and constraining mountain streams (D'Amico et al., 2000; D'Amico, 2004). A first goal of our study was thus to investigate how the pattern of time–activity budget and energy use in Dippers might vary under the very different natural flow regime of a nival mountain stream (>1300 m above sea level). To achieve this aim, we selected several streams within a water basin in The Pyrénées (Ossau valley; National Park of the Pyrénées; France) where natural flow regime is highly seasonal. These snowmelt-dominated streams result in pronounced and predictable runoff patterns. Water levels are highly variable oscillating predictably and markedly from very low values (summer) to very high ones (in spring during snowmelt), given also that Western-Pyrénées rivers are also characterized by high levels in autumn (due to heavy rainfall) and low levels in winter (rain being mobilized as snow). Moreover nocturnal temperatures fall below freezing during the winter and higher water levels are associated with higher velocity, depth and turbidity. Each of the 5 components of the NFR (i.e. magnitude, duration frequency, timing and rate of change — Poff et al., 1997) may influence directly or not behaviour and thus energetics of the Dipper. A second goal of this study was to put our data into a wider ecophysiological perspective by testing how Dippers conform to one of the two competing hypotheses existing to explain how endotherms manage their energy allocation seasonally in relation to environmental changes (e.g. Weathers and Nagy, 1980; Doherty et al., 2001; Bozinovic et al., 2004). Namely they are the 'reallocation' and the 'peak total demand' hypotheses, predicting, respectively, that total energy expenditure does not vary across seasons or is higher during the most constraining life stage or season, generally breeding or winter. We expected that Dippers should obey the rules of the latter one and further hypothesized that birds during periods of high water level should be inactive for much of the time, have low daily energy expenditure (DEE) and make extensive use of resting.

2. Methods

2.1. Study area

The study area included tributaries of three main streams, Valentin, Bious and Brousset, themselves being tributaries of the upper river Gave d'Ossau (Western Pyrénées; France). They are located within the fully protected area of the National Park of The Pyrénées. Only natural portions of the streams, *i.e.* situated above dams, were selected for bird surveys (see D'Amico, 2004 for further details on sites). Those natural segments of Valentin, Bious and Brousset streams are approximately 2, 6 and 10 km long, respectively, and range in altitude between 1360–1800, 1440–1790 and 1240–1770 m, respectively. The higher peaks of these watersheds culminate at 2885 and 2974 m respectively. These natural torrent streams are characterized by low water levels during winter and summer, but high discharge during snow-melt (April–June). Land use is mostly open pasture with scarce forest (*Fagus sylvatica* and *Abies alba*). With a maximum of 2.25 pairs/km and an overall mean density of 1.46 pairs/km, the recorded densities of breeding dippers at the study sites are among the highest in Europe (D'Amico and Hémery, 2003).

2.2. Estimation of time–activity budgets

Our methodology was strictly the same as previous, comparable studies (Bryant and Tatner, 1988; O'Halloran et al., 1990). We used known individuals (age, sex) in the colour marked population under study (see D'Amico and Hémery, 2003). Between October 1998 and August 2001, the same person observed (F.D.) and monitored each month birds activities using a portable tape recorder in combination with a telescope at a distance of 30–100 m. Observations were made at different locations (thus allowing for taking into account various channel substrate, flow type and bank profiles) of all bird territories, at all hours during daylight on predetermined days so that meteorological and hydrological conditions did not dictate its timing. As other authors we disregarded recordings lasting less than 1 minute and observations made of only one activity so that no individuals contributed disproportionately to the data (see below). Overall, 145 observations were made over 1528 min, with the longest record interval being 40.4 min (mean 10.8 min). Because we excluded data concerning juvenile birds ($n=15$), the present analysis was made on 130 recordings: 62 males, 52 females, and 16 birds of unknown sex.

To ensure unbiased comparisons, bird activities were categorized under the same main headings as in previous studies (Bryant and Tatner, 1988; O'Halloran et al., 1990), namely: *resting* (=time spent stationary during the day including standing quiet and alert, preening, singing, food manipulation and bobbing), *foraging* (=all walking activity, almost mainly devoted to pacing and pecking while feeding), *diving* (=all subsurface feeding) and *flying*. Birds were grouped where appropriate by month and split by sex and, more importantly, all activity data were weighted equally as published to reduce bias and warrant independence of the data (Bryant and Tatner, 1988; O'Halloran et al., 1990). We made the assumption that each breeding pair was involved in one clutch despite between 11.8 and 55.6% of the breeding pairs undertake a second clutch in The Pyrénées (D'Amico, Boitier and Marzolin, 2003). Our assumption may be however considered valid because during the study period, at the study sites (i.e. above 1200 m) none (1998), 16% (2000), and 24% (1999) of the local breeding pairs had a second clutch.

2.3. Modelling energy expenditure

Bryant (1997) has reviewed the energetics of free-ranging birds by summarizing the information on the Daily Energy Expenditure (DEE) of animals in the field, also known as Field Metabolic Rate (FMR; Nagy, 1989), which is typically determined by the doubly-labelled water method (Nagy, 1987; Speakman, 1997) or derived from Time–Energy Budgets (Bryant et al., 1985; Goldstein, 1988). DEE includes basal rate of metabolism (BMR), thermoregulation, locomotion, foraging, digestion, growth, reproduction, as well as all energy expenditures that eventually end up as heat production. In our study we calculated the Daily Energy Expenditure (DEE expressed in kJ d^{-1} ind^{-1}) of Dippers using the time–energy budgets obtained by incorporating our original time–activity data (see above) in the equation proposed by Bryant et al. (1985) and Bryant and Tatner (1988). We then derived the Average Daily Metabolic Rate (ADMR, J h^{-1} g^{-1}). The Basal Metabolic Rate (BMR) was calculated using allometric equations relating BMR to body mass (cf. the standard work by Aschoff and Pohl, 1970); as usually, it is called hereafter $\mathrm{BMR_{ap}}$. Among the different ways to assess the relationship between BMR and DEE or ADMR, here we expressed estimates of DEE as a multiple of $\mathrm{BMR_{ap}}$ (DEE/24 h $\mathrm{BMR_{ap}}$ — see Bryant and Tatner, 1988; Bryant and Tatner, 1991; Bryant, 1997; McKechnie and Wolf, 2004 for further details). The ratio DEE/24 h $\mathrm{BMR_{ap}}$ is called M in some studies (Bryant and Tatner, 1991; Bryant, 1997) but is more generally known as the DEE/BMR or FMR/BMR ratio (Koteja, 1991; Ricklefs et al., 1996).

Given that the requirement for food and the time available for gathering it both determine the minimum average rate at which food must be obtained to achieve daily energy balance we also calculated the required foraging rate (E_{req}) and the observed rate of energy gain (E_{obs}) (Bryant and Tatner, 1988). E_{req} is DEE divided by the active daylength for birds whilst the observed rate of energy gain (E_{obs}) describes the mean rate (kJ h^{-1}) at which energy is seen to be obtained from gathering food and calculated by dividing DEE by the total time spent feeding by birds (i.e. total time spent diving + foraging).

As a consequence, the ratio $E_{\mathrm{obs}}/E_{\mathrm{req}}$ indicates how much faster observed feeding rates are in relation to minimum required feeding rates. If birds gather food at a rate just sufficient to balance their energy budget then this ratio is equal to 1. Of course this strategy is risky and it is expected that $E_{\mathrm{obs}}/E_{\mathrm{req}}>1$.

2.4. Environmental data

On the day we made behavioural surveys, we measured directly air temperature, water temperature and water stage (=depth of water column) using probes and limnimetric scales at each river segment under study. For the purpose of analysis, we grouped water stage values into 5 classes (1: 1–24 cm; 2: 25–49 cm; 3: 50–74 cm; 4: 75–99 cm and 5: 100–149 cm). To ascertain that those data conformed to long-term hydrological characteristics of the rivers under study, we compared our local data to the long-term water stage dataset (1979–1996) available from the nearest automatic gauging station (Oloron Sainte-Marie; no Q6142910; situated 50 km downstream) operated by the Direction Régionale de l'Environnement (DIREN Aquitaine; DataBank HYDRO; http://www.hydro.eaufrance.fr/). Prior to statistical analysis, data were standardized to enable comparisons between streams of different size and data of different years. Daylength was determined from documented times of sunrise and sunset in south France (values given in Appendix).

3. Results

3.1. Natural regime flow

The annual pattern during the study period was very similar to the long-term one (Fig. 1). Maximum height was recorded in May whatever the site. As said in the section Introduction, water levels were highly variable oscillating seasonally from very high values during snowmelt (between April and June) and very low values (summer). The flow was also characterized by relatively high levels in autumn (November at rainfall period)

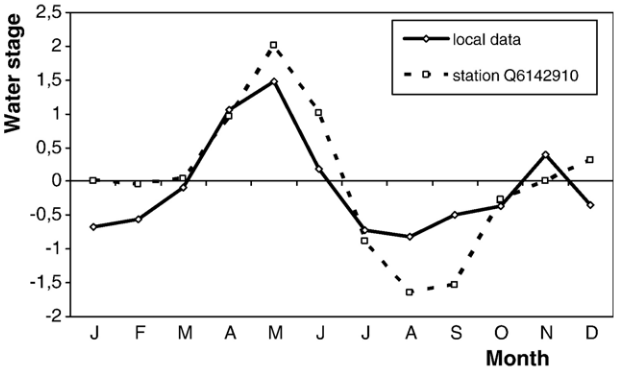

Fig. 1. Natural flow regime in The Pyrénées: annual pattern in water stage variation (standardized data) recorded locally at study sites (upper Ossau valley; 1998–2001 — solid line) and obtained from the DataBank HYDRO at the nearest automatic gauging station (no Q6142910) operated by the DIREN Aquitaine (lower Ossau valley; 1979–1996 — dotted line).

and low levels in winter (rain being mobilized as snow between December and March at local upstream study sites). Not surprisingly, winter standardized values were greater at station no Q6142910 than at local station, the former one being situated well downstream the latter one.

3.2. Time–activity budgets

Foraging and resting were the most variable behavioural categories across month (Fig. 2-A,C). They consistently displayed opposite trend, foraging being the highest time-consuming activity especially during winter whilst resting was very low during winter but the prevailing activity in May. Maximum time spent resting was 74.4% of the active-day. Diving, flying and other activities showed no peculiar pattern (Fig. 2-B,D,E). Mean time spent diving averaged 10% of the active-day across the year and peaked at 18% of the active-day in February (Table 1); this behaviour was more prominent in late winter and spring and rare during summer (moult period). Across year mean time spent roosting varied between 32% and 66% of the 24-hour day (Table 1).

Time–activity budgets differed significantly between month for each of the behavioural categories identified (Table 2). By contrast, time–activity budgets for male and female Dippers did not differ significantly excepted for resting activity (Table 2), this behaviour being less prominent in females. The interaction term between sex and month or sex was never significant.

3.3. Effects of flow variation

Apart for the 'other' activities, all behavioural categories showed marked relationship to water stage variation. Mean time spent foraging in the active-day decreased with increasing water levels (Fig. 3-A) meanwhile time spent resting increased regularly (Fig. 3-C). Variation in diving (Fig. 3-B) and flying (Fig. 3-D) displayed a humped-shape pattern, mean time being the highest for intermediate (class 3, i.e. 50–74 cm height) water levels. Polynomial regression (diving and flying) or linear regression (foraging and resting activities) indicated a significant relationship ($p < 0.001$) between behaviour and water stage.

3.4. Energy expenditure

Mean daily energy expenditure (DEE derived from time–energy budgets) showed similar pattern in variation between months (Fig. 4). DEE regularly varied between 240 and 280 kJ d^{-1} ind^{-1} between January and June whilst decreasing to a

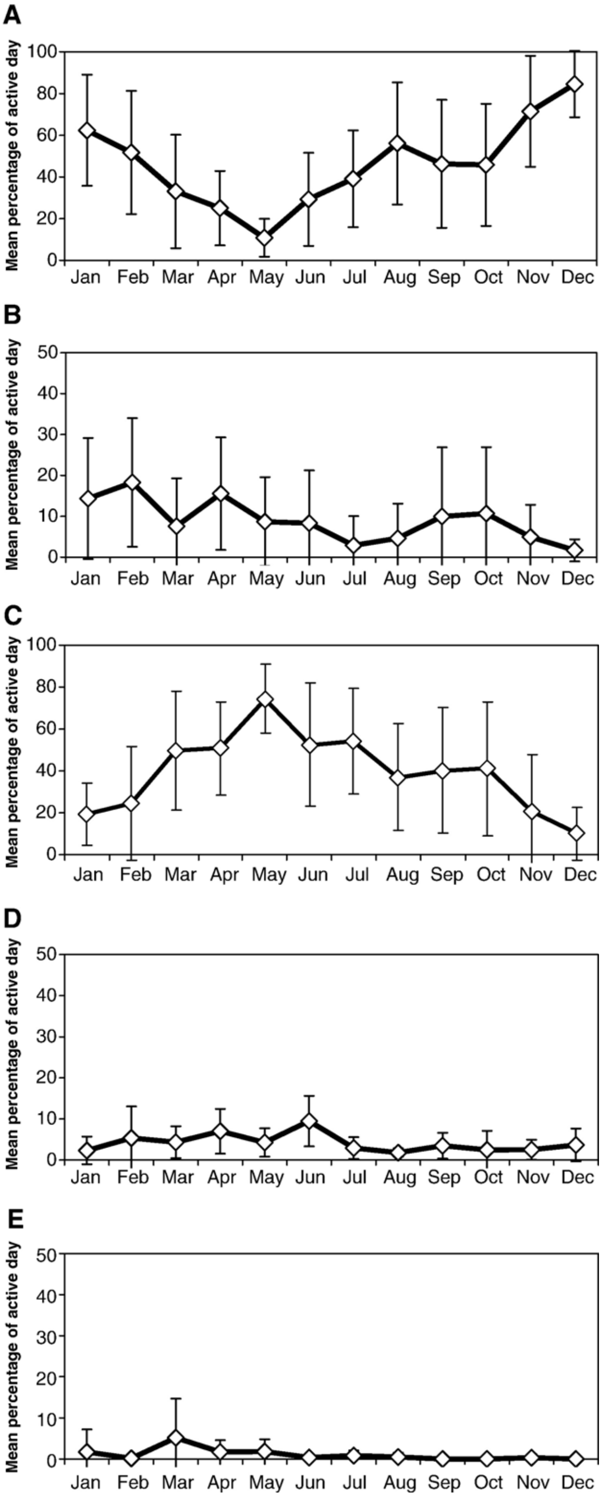

Fig. 2. Mean (±S.D.) time spent each month by Dippers (males and females pooled) on natural streams in The Pyrénées (Ossau valley; 1998–2001) in: A) foraging, B) diving, C) resting, D) flying and E) other activities.

Table 1
Time–activity budgets of adult Dippers in the Pyrénées (Ossau valley; 1998–2001) according to month in case of one brood

	% Active-day					% 24-hour day							
	Foraging	Diving	Resting	Flying	Other activities	Roosting	Foraging	Diving	Resting	Flying	Other activities	(*n*)	min
January	62.4	14.4	19.2	2.3	1.7	64.4	22.2	5.1	6.8	0.8	0.6	12	113.2
February	51.7	18.3	24.6	5.3	0.1	57.8	21.8	7.7	10.4	2.3	0.1	11	116.4
March	33.1	7.6	49.8	4.4	5.2	50.6	16.3	3.8	24.6	2.2	2.5	12	103.7
April	25.0	15.5	50.8	7.0	1.7	42.6	14.4	8.9	29.2	4.0	1.0	18	143.0
May	10.8	8.7	74.4	4.3	1.8	35.8	7.0	5.6	47.8	2.7	1.2	16	234.7
June	29.3	8.3	52.6	9.5	0.4	31.9	19.9	5.7	35.8	6.5	0.2	9	82.8
July	39.1	2.9	54.3	2.9	0.8	33.5	26.0	1.9	36.1	1.9	0.5	9	145.2
August	56.1	4.6	37.0	1.8	0.5	35.5	36.2	3.0	23.8	1.2	0.3	7	119.2
September	46.3	10.0	40.3	3.5	0.0	47.4	24.4	5.2	21.2	1.9	0.0	9	59.6
October	45.8	10.7	41.0	2.5	0.0	55.1	20.6	4.8	18.4	1.1	0.0	14	149.1
November	71.5	4.9	20.8	2.5	0.3	62.3	26.9	1.9	7.8	0.9	0.1	8	84.2
December	84.5	1.7	10.1	3.7	0.0	66.3	28.5	0.6	3.4	1.2	0.0	5	51.5

plateau the rest of the year, around 200–220 kJ d^{-1} ind^{-1}. If we split those data into two groups (January–June versus July–December), DEE differed significantly (Mann–Whitney test; $W=57.0$, $p=0.0051$). No significant differences in ADMR and DEE were found between sexes (Mann–Whitney test, $p>0.05$). DEE was not linearly correlated to water stage ($R^2=24.8\%$, $p=0.1$). *M,* the DEE/BMR_{ap} ratio, varied monthly across the year; the maximum ratio value peaked at 4.33 for males in April and at 4.58 and 4.55 for females in February and April respectively (Table 3). *M* was also high (=4.46) in females during June (Table 3). Contrary to Bryant and Tatner (1988), we didn't calculate ADMR, DEE and *M* for nestling-feeding parents with two broods.

3.5. Rates of energy gain

Rates of required (E_{req}) and observed (E_{obs}) energy gain varied consistently between month or stages of the annual cycle. For males and females, E_{obs} peaked in spring (maximum value in May). Variation in the ratio E_{obs}/E_{req} followed the same pattern (Fig. 5). This ratio E_{obs}/E_{req} did not differ significantly between sexes (Mann–Whitney test, $p>0.1$) for Pyrenean Dippers whatever the month.

4. Discussion

4.1. Time–activity budgets (TABs) and feeding rates match the natural regime flow (NFR) but energetics cycle do not…

A remarkable finding of our study is that TABs analysed per month are easily superimposed to the natural hydrogramm flow regime. Because Dipper behaviour is well synchronized with flow patterns, this result sticks perfectly to the main prediction of the paradigm of the NFR (Lytle and Poff, 2004). For the first time we demonstrated that the 'resting' activities temporal pattern (Fig. 2-C) exactingly followed the temporal pattern of the monthly flow regime (Fig. 1) and that it was strictly opposite to the temporal pattern of 'foraging' (Fig. 2-A). These conclusions are well rehearsed in the graphics depicting the relationships to water stage (Fig. 3-A,C). Clearly, Dippers in The Pyrénées spent less time foraging at high discharge level (snowmelt period) but more time resting (up to 75% of the active-day). The pattern in 'diving' activity showed no visible temporal trend (Fig. 2-B) and was apparently not so clearly related to the natural hydrogramm (Fig. 1). Indeed, it is easy to explain given the subtle relationship existing between time spent diving and water stage: diving increases with increasing discharge of the river (rate of flow expressed in m^3 s^{-1}) up to a point (water stage class 3 in Fig. 3-B) where it falls back. This relationship was already described in Welsh rivers by O'Halloran et al. (1990). These set of observations raise the question of how Dippers get food when discharge increases (Da Prato, 1981; D'Amico et al., 2000 ; Taylor and O'Halloran, 2001) and especially when the flow is at its maximum leading to what we present below as a paradox. It is proved that Dippers may cease feeding entirely during short flow spates (Da Prato, 1981) and that Dipper diet composition is immediately affected by modifications of the water flow (Taylor and O'Halloran, 2001) ; yet there are no published data on the behaviour and diet of Dippers during prolonged spates or flood events.

Surprisingly, our study failed to demonstrate that annual pattern in DEE match the NFR. The key finding is that annual pattern in DEE clearly exhibited two periods, with statistically different values. The first one runs from January to June (Fig. 4) and is described by oscillating values with low amplitude, the second one being characterized by a 'plateau' with very slowly increasing values. This annual pattern was absolutely not linked

Table 2
Two-way analysis of variance for categories of time–activity budgets in Pyrenean Dippers (Ossau valley; 1998–2001) with month and sex in case of one brood

	Factors	*F*	*df*	*P*	Interaction	*F*	*df*	*P*
Foraging	Month	4.77	11	0.001	Month * Sex	0.81	11	0.627
	Sex	2.60	1	0.110				
Diving	Month	1.85	11	0.057	Month * Sex	0.99	11	0.462
	Sex	0.73	1	0.396				
Flying	Month	2.72	11	0.005	Month * Sex	0.94	11	0.508
	Sex	0.26	1	0.609				
Resting	Month	5.87	11	0.001	Month * Sex	0.97	11	0.483
	Sex	15.39	1	0.001				
Other activities	Month	2.20	11	0.021	Month * Sex	0.34	11	0.975
	Sex	0.39	1	0.532				

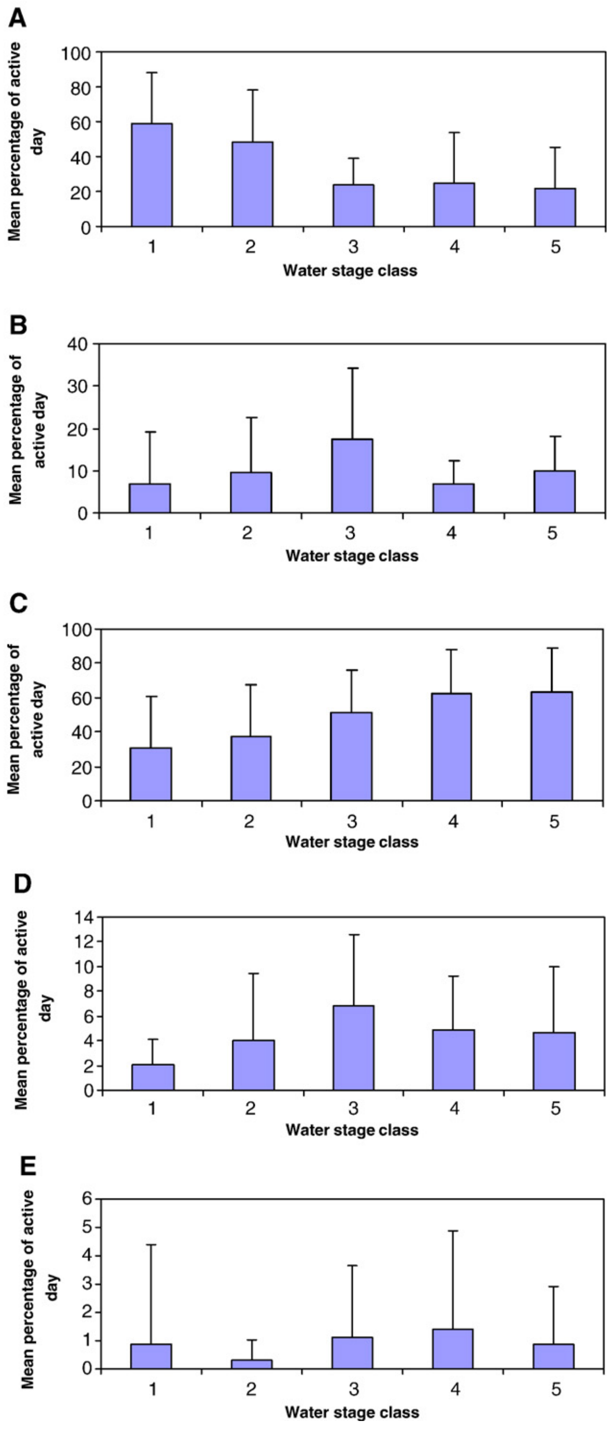

Fig. 3. Relationship between water stage (grouped into 5 regular intervals: class 1: 1–24 cm; class 5: 100–149 cm) and mean (±S.D.) percentage of the active-day spent in each behavioural category (A — foraging, B — diving, C — resting, D — flying and E — other activities) by Dippers (males and females pooled) on natural streams in The Pyrénées (Ossau valley; 1998–2001).

to the natural annual regime flow (Fig. 1) in the sense that the high discharge period (snowmelt) was not tracked by the DEE changes. Low values of DEE were observed during low water level period (July–August) which corresponds to the moulting period for Dippers. Some of the patterns of energy expenditure of Dippers are rather well known and the influence of some intrinsic and environmental factors on DEE have been described: ambient temperature, food, body mass, body size, age, percentage time flying and active are significantly correlated (Bryant et al., 1985; Bryant and Tatner, 1988; O'Halloran et al., 1990; Bryant and Tatner, 1991). Sun and wind are suspected to have no effects. Moreover, Bryant et al. (1985) showed that variation in DEE during winter for Dipper was merely a consequence of changes in the nature and duration of energy-costly activities. It is also known that dominant Dippers have higher metabolic rates but that the energy cost of dominance is small and unlikely to affect energy balance (Bryant and Newton, 1994) neither survival (Bryant and Newton, 1996). Similarly, moult in Dippers doesn't increase DEE neither BMR (Brown and Bryant, 1996). Yet nothing is known on reserve storage and fat use in this species. Interestingly, roosting Dippers at night display an unexpected slight heat loss through plumage to surrounding environment (Davenport et al., 2004). Consequences on the daily and annual energetics of the species are unknown. So far, our study was not intended to address these issues and subsequent discussion is done with this lack of knowledge in mind. All the monthly DEE estimates were derived in our study from time–energy budgets for Pyrenean Dippers using calibrated methodology (Bryant et al., 1985) and shortcomings of the approach have already been detailed in previous comparable studies (Bryant et al., 1985; Bryant and Tatner, 1988; O'Halloran et al., 1990).

It is puzzling to note that the feeding rates followed in some ways the natural flow regimes. In the Pyrénées, whatever the sex of the Dipper in this population, E_{obs} peaked in spring (maximum value in May i.e. at snow-melt) and during the period of nestling rearing and fledgling attending. Males and females Dippers displayed (Fig. 5) high values of the ratio E_{obs}/E_{req} at maximum snowmelt-borne discharge in May and, by contrast, low values near the critical threshold of 1.0 during winter (November–February). High values usually imply rapid feeding rates that could directly be explained by easily accessible food or made compulsory by competing behaviours (Bryant and Tatner, 1988). That highest value corresponded to maximum discharge is puzzling in the sense that it is unlikely that food availability or abundance is at its maximum given that highest discharge imply highest water depth, velocity and turbidity impeding birds to feed easily (D'Amico et al., 2000). Indeed, at this time (May) of the year, birds do forage at the minimum level (ca 10% of the active-

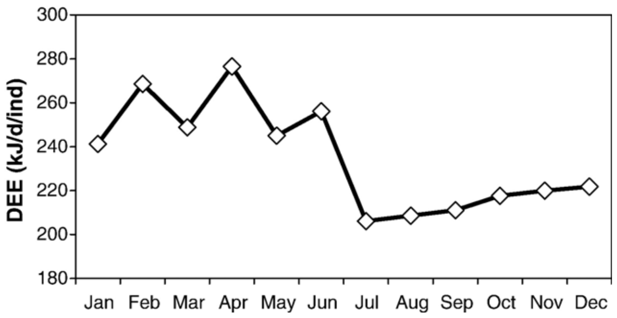

Fig. 4. Mean daily energy expenditure (DEE; kJ d^{-1} ind^{-1}) by adults Dippers (males and females pooled) on natural streams in The Pyrénées (Ossau valley; 1998–2001) according to month.

Table 3
Estimated energy expenditure by Dippers in the Pyrénées (Ossau valley; 1998–2001)

	Males			Females		
	ADMR	DEE	M	ADMR	DEE	M
	$J\ g^{-1}\ h^{-1}$	$kJ\ d^{-1}\ ind^{-1}$		$J\ g^{-1}\ h^{-1}$	$kJ\ d^{-1}\ ind^{-1}$	
January	172	272	4.12	161	214	3.68
February	175	278	4.22	200	266	4.58
March	164	261	3.95	180	240	4.13
April	180	286	4.33	199	264	4.55
May	162	258	3.91	178	236	4.06
June	158	251	3.80	195	260	4.47
July	134	212	3.22	147	195	3.36
August	140	222	3.37	145	193	3.32
September	137	217	3.30	158	210	3.61
October	148	234	3.55	151	200	3.45
November	150	238	3.61	156	207	3.56
December	150	237	3.60	154	205	3.53
Mean (±S.D.)	155.9± 15.2	247.2± 24.2	3.7± 0.4	163.6± 20.7	227.2± 24.6	3.9± 0.5

Average Daily Metabolic Rate and Daily Energy Expenditure did not differ significantly between sexes (Mann–Whitney test, $P>0.05$) for Pyrenean Dippers (Ossau valley; 1998–2001) according to month in case of one brood. M is the ratio DEE/24 h BMR_{ap} (Bryant and Tatner, 1991; Bryant, 1997).

day) and spend maximum time resting (ca 80%) thus relying also upon diving (ca 10%). These observations raise what we question below as being an interesting paradox. On the contrary, best explanation for lowest observed values of the ratio E_{obs}/E_{req} during winter are likely triggered by daylength, being short in winter and thus allowing for less time foraging or diving. To summarize, Pyrenean Dippers are likely to be at highest energy stress during winter and paradoxically at lowest energy stress during high snowmelt spates when food is expected to be difficult to obtain obliging individual birds to spend most of the day resting (Da Prato, 1981; Taylor and O'Halloran, 2001) as discussed above. To get further insights in the rates of energy gain, we used published results to draw a synthetic graph (Fig. 5) displaying compared annual variation in the ratio E_{obs}/E_{req} for the available populations so far studied (Pyrénées, this study; Wales, O'Halloran et al., 1990 and Scotland, Bryant and Tatner 1988). Whatever the sex, it shows consistently that patterns differ with the population; in the Pyrénées, the highest values of the ratio E_{obs}/E_{req} occurred at snowmelt-borne maximum discharge in May whilst in Wales they peaked in October (Fig. 5). It will be useful to examine in the future those contrasting annual pattern in relation to the regional hydrogramms of these populations and in the context of the NFRP.

4.2. 'Peak total demand' versus 'reallocation' hypothesis

Food abundance and physical environmental conditions (especially temperature) in nature influence the rates at which animals can acquire and expend energy (Kenagy et al., 1989; Corp et al., 1999). Organisms are thus continually challenged to maintain energetic homeostasis (Johnston and Bennett, 1996). In rivers — besides temperature — level, velocity, depth and turbidity of running water are critical physical stressors (D'Amico et al., 2000) all of them acting at different time scales, some on a seasonal and predictable basis as predict the NFRP. Of the two competing hypotheses telling how birds (and mammals) cope with environmental changes and pressure to seasonally manage their energy allocation (e.g. Weathers and Nagy, 1980; Doherty et al., 2001; Bozinovic et al., 2004), it appeared from our results that Dippers subscribed best to the 'peak total demand' hypothesis stating that total energy expenditure vary across seasons and must be higher during the most constraining season or period (generally breeding or winter). This is well illustrated by the significantly higher DEE during winter and spring (Fig. 4). To help understand why time–activity budgets and energy use might differ across the different life stage of Dippers and with the pattern in runoff, we propose two alternative hypotheses. When facing harsh conditions (successively cold temperature and high discharge) we would expect that Dippers could either follow an energy-minimisation strategy (by choosing low-cost feeding strategies or making extensive use of resting) either adopt an energy-maximisation strategy (by relying on presumably more efficient but more costly feeding strategy such as diving or limiting time resting). The energetic consequences would be respectively low and high daily energy expenditure (DEE). Modelled data derived from the field observations indicated that none of the two hypothesis is fully satisfied. During snow-melt, Dippers paradoxically exhibit predictions of both strategies displaying high energy expenditure but spending huge time resting and showing no prominent preferred feeding strategy (foraging = diving). It is no doubt anyway that Dippers under those harsh conditions must meet their daily food requirement in a very efficient way, during short feeding intervals for example whatever the feeding strategy

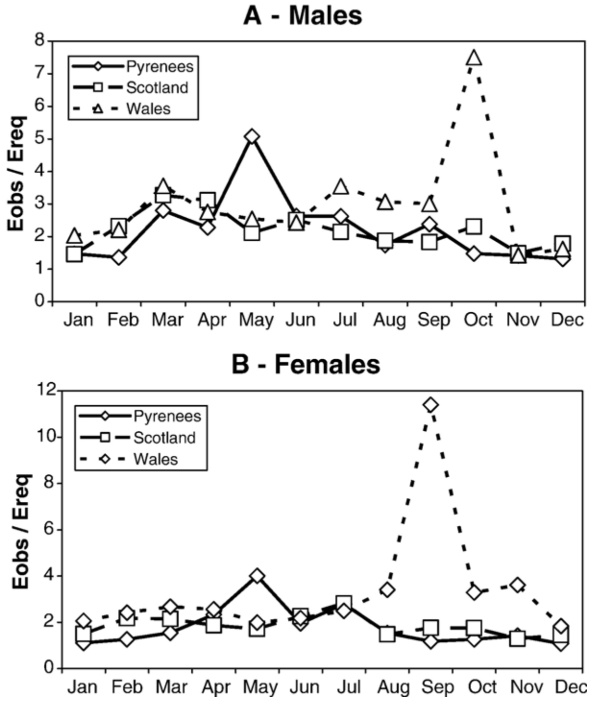

Fig. 5. Compared mean monthly values of the ratio of observed rate of energy gain to minimum required rate of energy gain (E_{obs}/E_{req}) by males and females Dippers: The Pyrénées (Ossau valley; *this study*); Scotland (drawn from data in Bryant and Tatner, 1988) and Wales (drawn from data in O'Halloran et al., 1990).

(foraging or diving) as do the arctic Cormorants by maximizing foraging efficiency through a single intensive dive bout (Grémillet et al., 2001). This hypothesis is further sustained by the fact that E_{obs} and the ratio E_{obs}/E_{req} were at a maximum at that time in our Dippers, indicating a high feeding efficiency. So far, those contrasting findings are difficult to explain and will deserve further modelling investigations to disentangle what appears as a paradox.

5. Conclusions

A question remains open: what is the best currency to measure "energy stress" in Dippers coping with the natural constraints of their habitat, especially the NFR? Since Drent and Daan (1980) published their seminal paper on 'the prudent parent', the ratio between DEE (=FMR) and BMR (the 'sustained metabolic scope' or 'sustained working rate') has repeatedly been given importance when assessing the energy loads of birds (Bryant and Tatner, 1991; Bryant, 1997) and other groups of animals. A maximum value for the ratio DEE/ BMR of approximately 4.0 to 4.5 was also claimed (Drent and Daan, 1980), although some studies have shown that DEE may be as high as seven times the BMR (Bryant and Tatner, 1991; Hammond and Diamond, 1997). In our study, calculated values of M (expressing here the ratio DEE/BMR_{ap}) varied across the year with maximum ratio values peaking at 4.33 for males and at 4.58 for females. In their comparative study, Bryant and Tatner (1991) showed that energy expenditure of free-living Dippers may increase up to 5 times the BMR. It is even possible that M ratio for adult females feeding youngs increase up to 8.44 times the BMR (Bryant and Tatner 1988). The idea of a maximum limit to the ratio between DEE and BMR (whatever its magnitude) has originated from the suggestion that there could be a functional link between DEE and BMR (Nagy, 1987; Koteja, 1991; Ricklefs et al., 1996; Hammond and Diamond, 1997). Recent studies show that DEE and BMR could change independently of each other and in opposite ways (Bech et al., 2002) and also that there is no functional coupling between them (Hammond and Diamond, 1997). Obviously, despite there is no satisfactory explanation for this apparent paradox the DEE/ BMR ratio is probably not a good indicator of energy stress. Bech et al. (2002) suggest that energy stress in an organism depends more on the ratio between energy intake and expenditure than on the actual level of energy expenditure. Thus, the ratio E_{obs}/E_{req} could still be a useful currency and *a fortiori* in the case of Dippers, also because the published studies on Dipper energetics do use it, enabling for comparisons among contrasting environments and NFRs.

The challenge is now to explore the possible occurrence of compensatory shifts among various categories of energy expenditure that allow Dippers to manage their overall energy balance by minimizing expenditure at some time of the year or life stage of the annual cycle. Such question arise from the strong major shift in total levels of modelled DEE in opposition to what reveals indicators of feeding efficiency (E_{obs}/E_{req} ratio) and energy stress (M ratio). In this study we made the oversimplifying assumption that Dippers engaged in a unique clutch. Indeed, Pyrenean Dippers at this altitude have two breeding strategies (one or two brood), with variable reproductive success and timing of breeding spreads over a long period (D'Amico et al., 2003). Given the extra-costs of egg laying, incubating and provisioning nestlings and fledglings (Bryant and Tatner, 1988, Bryant, 1997) and because foraging parents are constrained by complex interactions between prey size, energy demands and foraging efficiency there is a need to investigate how breeding might affect annual cycle energetics in Dippers and examine it for example in the general framework of the "feeding constraint hypothesis" (Slagsvold and Wiebe, 2007).

For now, we stay with the central conclusion that time–activity budgets and energy use in Dippers are largely dictated by the pattern of temporal variation in river flows, thus verifying a major assumption of the NRFP. The emerging paradox highlighted above poses further fundamental questions on adaptive energetics (Mathias et al., 2004) and the underlying modes of adaptation (here, how Dippers have evolved a behavioural strategy for coping with extreme flows and depending on natural flow regimes) and how they may decide whether individual birds can survive flow regime alteration. As such, diving might be the main factor shaping physiology and thus energetics of the Dipper and this species should prove to be an excellent model to further test the so-called 'diving paradox' (Davis et al., 2004) and, in the context on our framework, to develop more innovative approaches on the influence of flow alteration on the energetics of this species. More generally, these crucial lessons will serve the overwhelming challenge of maintaining native birds (especially those at risk — see Nilsson and Dynesius, 1994; Tyler and Tyler, 1996) and more generally speaking biodiversity in human-altered rivers and streams (Dynesius and Nilsson, 1994; Lytle and Poff, 2004).

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Appendix. Data on mean ambient temperature (°C) at night (T_{aN}) and during the day (T_{aD}) and active daylength (t_D) for calculating daily energy expenditure

	t_D (h)	T_{aD} (°C)	T_{aN} (°C)
January	9.55	0.20	−0.30
February	11.12	0.10	−0.40
March	12.85	3.50	3.00
April	14.78	5.50	5.00

Appendix (*continued*)

	t_D (h)	T_{aD} (°C)	T_{aN} (°C)
May	16.42	9.20	8.70
June	17.35	12.20	11.70
July	16.95	14.90	14.40
August	16.47	14.90	14.40
September	13.63	12.90	12.40
October	11.78	8.20	7.70
November	10.05	3.60	3.10
December	9.10	1.00	0.50

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