Individual and population energetics of a lizard on a Mediterranean islet

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Summary. Population density in the lacertid lizard *Podarcis lilfordi* on the Mediterranean islet of Nitge, Menorca, Balearic Islands, was found to be 12190 ind · ha^{-1} (SE, ±2135), exceeding densities reported for other island or mainland lizard populations. Field metabolic rates in *P. lilfordi* were measured by the doubly labeled water method, allowing estimation of a population metabolizable energy demand of 13.86 MJ · ha^{-1} · day^{-1} – only 9.8% of that for a theoretical mammal population of the same body mass and density. Energy demand was considerably higher than that estimated for other lizard populations, primarily due to high population density but also because of high individual daily energy expenditure (1255 KJ · day^{-1}; body mass = 5.13 g). Field metabolic rates were partitioned into maintenance and activity components by respirometry of captive animals at field body temperatures. Activity metabolism formed the main component (77.4%) of total respiratory metabolism, resulting from a combination of long daily activity periods (ca. 12 h), and greatly elevated metabolism during activity (5.7 times greater than resting levels). It is hypothesized that low food availability per individual constrains the time-energy budget of this species, obligating long periods of intense foraging.

Key words: Balearic islands – Energy expenditure – Islet – Lizard – Population density

Field energy requirements of reptiles are only approximately 6% of those of endotherms of the same size (Nagy 1982, 1987). For a given biomass they therefore account for a much smaller proportion of the energy flow through a community. Reptiles may, however, reach greater population densities and thus make a highly significant contribution to the energy dynamics of an ecosystem. Some of the highest known reptile densities are those for small lizard species on tropical islands, where observations of

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between 1 and 5000 animals per hectare are not uncommon (Andrews 1979; Bennett and Gorman 1979; Brooke and Houston 1983; Ruibal and Philibosian 1974).

A relaxation of the normal predation pressures appears to at least partially explain the high densities of island lizard populations, a view supported by observed declines in densities on islands where predators have been introduced (Case and Bolger 1991). If this is the case, it might be expected that individual food requirements/food availability will play an important role in determining population densities in some island lizards.

The energetics of insular lizard populations are therefore of interest at both the individual and population levels. This was highlighted by Bennett and Gorman (1979) who demonstrated that, as a result of their high biomass, a lizard community on a Caribbean island had a greater energy demand than published values for small mammal communities. Estimates of energy demand in this study were achieved by integration of field studies of population densities, time budgets and thermal relations with metabolic measurements in the laboratory. More recently, the development of the doubly labeled water method (Nagy 1980) has revolutionized studies of field metabolism by allowing CO_2 production to be directly measured in free-ranging animals (Nagy 1989; Speakman and Racey 1988).

This study uses the doubly labeled water method to determine field metabolic rates (FMR) activity costs, and population energy demand in summer in the lacertid lizard *Podarcis lilfordi fenni* (Eisentraut 1928) from the islet of Nitge, Menorca, Balearic Islands. *P. lilfordi* became extinct on the main island of Menorca (probably around 5000 years ago) due to the introduction of predators (Eisentraut 1949; Mertens 1957) and/or a congeneric competitor (Alcover et al. 1981). It currently survives on at least 14 of the small islets situated between 30 and 1000 m from the Menorcan coast, where it may reach very high population densities (Pérez-Mellado 1989). Such high densities are found on Nitge which is located about 450 m from the central northern coast of Menorca and has a surface area of 106250 m^2 (Pérez-Mellado

1989). It reaches a maximum altitude of 26 m, is southerly inclined, and ca. 90% covered by vegetation comprising four species; *Chrithmum maritimum, Allium ampeloprasum, Atriplex portulacoides* and *Portulaca americana* (Pérez-Mellado 1989). Nitge is one of the least disturbed of the Menorcan islets, being uninhabited and having no easy embarkation point for water-craft. Also, there is no evidence of rats there (or other mammals), which appear to reduce *Podarcis lilfordi* densities on some of the other Menorcan islets (Pérez-Mellado, unpubl. data).

Materials and methods

A line transect method (Burnham et al. 1980) was used to calculate the population density of *P. lilfordi* in Nitge in July 1991. Perpendicular distances were recorded between sighted lizards and linear transects walked at periods of maximum activity across the entire islet. The accuracy of this method depends on detection of all animals situated on the central line of the transect, with some perpendicular distance function giving the detection probability either side of the line (Burnham et al. 1980). The probability of detection function was determined using a Fourier series, which enables good estimate repeatability in Menorcan islet lizards (Pérez-Mellado 1989). Estimates of population density and associated variance were obtained from three replicate transects conducted in Nitge in July which were combined using a jackknife procedure (Burnham et al. 1980).

For the doubly labeled water study, lizards were caught by noosing, uniquely toe-clipped, measured from snout to vent (to 0.05 mm) and then weighed to 0.01 g on a portable electronic balance (A & D Co. Ltd). A blood sample was collected (ca. 56 μl) from the infra-orbital sinus of one of the captured individuals using eight 10-μl micropipettes which were then flame-sealed, and the animal released. These samples were used to determine background ^{18}O and deuterium concentrations at the start of the study. Low recapture rates were expected due to the dilution effect of the high population densities so a large number (53) of animals were labeled by intra-peritoneal injection with 0.0095–0.0190 ml of water containing 39.41 atom per cent (APE) ^{18}O and 23.99 APE deuterium. Labeled animals were left in small cotton bags in the shade for approximately 3.5 h to allow for isotope equilibration. Blood was sampled as previously described, although smaller volumes (28–42 μl) were collected if the animal appeared to be greatly stressed by the procedure. A further 12 animals were toe-clipped, measured and weighed but not injected with doubly labeled water or blood sampled, to check for possible stress-induced weight change effects over the subsequent study period. All lizards (53 + 12 = 65) were given a small paint mark on the upper dorsum to facilitate recognition at a distance, and released close (< 5 m) to the point of capture.

Of the labeled lizards 11 were recaptured by hand or noose 8–10 days after labeling. Each was reweighed and 56 μl of blood collected and sealed in micropipettes (as above). An additional animal was recaptured and blood samples collected to check for changes in background ^{18}O enrichments during the study period (Speakman and Racey 1987).

Hydrogen and carbon dioxide gases were prepared in duplicate from each blood sample, and respective deuterium and ^{18}O enrichments determined by mass spectrometry. All analyses were carried out by the Centrum voor Isotopen Onderzoek, Rijksuniversiteit Groningen, Holland. Methods are more fully described in Masman and Klaassen (1987).

Recaptured lizards were frozen for transport back to the laboratory where they were thawed, weighed, and dissected to determine sex. Stomach contents were analyzed and replaced in the carcass (dietary variations in this species will be dealt with in a future paper, so results of stomach contents analyses will only be mentioned briefly here). Specimens were desiccated to constant mass in an oven at 65° C to determine body water content.

Initial body water volumes were determined from desiccated masses, assuming constant mass-specific water composition during the study period. Individual field metabolic rates (FMR) were determined using the Lifson and McClintock (1966) equation for linearly changing body water volumes, and were based on a thermal equivalent of 25.7 J · ml CO_2^{-1} (Nagy 1983).

Environmental temperatures and humidities in Nitge were averaged over 2-min intervals during two 24-h periods (at the beginning and end of the doubly labeled water study) and stored for later analysis using a digital datalogger (DGT Ltd.).

Five *P. lilfordi* were captured from Nitge at the end of July and transferred to the laboratory for determination of resting metabolic rates. They were maintained for 4 months at light/dark regimes corresponding to natural photoperiods. Controlled feeding of *Tenebrio* larvae ensured that all lizards maintained, or showed small gains on capture weights. Eight days before beginning the oxygen consumption measurements, the photoperiod was set to a 14:10 hour light:dark regime, and night temperatures to 25° C (i.e., similar to July conditions in the Balearic Islands). A previous study detected no differences among resting metabolic rates (above 15° C) of individuals of the closely related *Podarcis hispanica* which had undergone different seasonal acclimation treatments (Patterson and Davies 1978).

Resting rates of oxygen consumption were determined using an open-flow system, consisting of an oxygen analyzer (Applied Electrochemistry S–3A) connected to a chamber (gas-tight 60-ml syringe) containing the animal. The air flow-rate (10.0 ml · min^{-1}) through the chamber was controlled using a high precision mass flow controller (Sierra Inst. Sidetrak 840). The two channels of the analyzer continuously monitored incurrent and excurrent air from the chamber. A cooled incubator (Sony Gallenkamp INL–411) maintained the chamber temperature within 0.5° C of 33.5° C day (corresponding to the preferred body temperature of *P. lilfordi* from Nitge – Pérez-Mellado and Bauwens, unpubl. data), and 25° C nighttime test temperatures (mean shaded-rock temperature during the period of no activity). Lizards were fed and placed in the chamber around midday, being removed the following day. Oxygen consumption was averaged over 5-min periods by a BBC microcomputer (Acorn Computers Ltd). Even slight activity by the animal had a considerable effect on resting rates of oxygen consumption, so minimum rates over ten minute periods were used rather than the mean day and night values. Values were corrected to STPO, energy equivalents were determined using 19.3 J · ml O_2^{-1} (Nagy 1983).

Results

P. lilfordi were observed to be active on Nitge between 0500 hours and 1800 hours (GMT; for local time add 2 h), although main population activity was between 0530 hours and 1730 hours. Temperatures of model *P. lilfordi* exposed to the sun averaged 36.92 ± 0.36° C (unless specified otherwise, ± values are standard errors of means) during the main population activity period, and 25.07 ± 0.09° C (below vegetation) during the period of low/no activity. Respective maximum (day, shade) and minimum (night) temperatures and humidities were 33.3° C, 22%, and 23.0° C, 91%.

Examination of the gonads of the 11 recaptured animals that had been labeled with isotopes (and abdominal palpation of all captured females) indicated that the population was not reproductively active during the study. Stomach contents consisted mostly of insects

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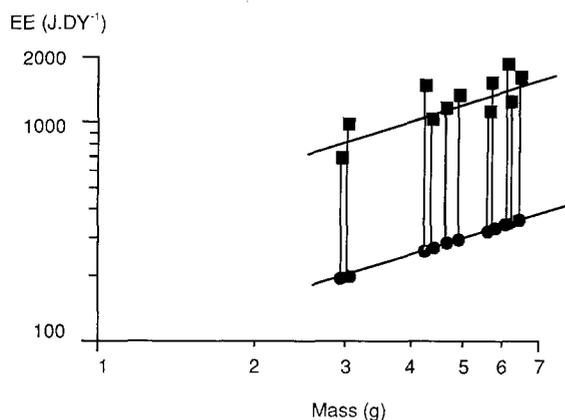
Fig. 1. Field metabolic rates (FMR) ■ and estimated daily maintenance metabolism (MEE) ● in *P. lilfordi*. *Vertical lines* join MEE to FMR for each individual. The FMR/body mass regression is given by; $FMR = 342.0 \cdot g^{0.7900}$ J $\cdot$ day^{-1} ($F_{1,10} = 14.05$, $P < 0.005$), while the MEE/body mass slope was 0.779, as determined by a previous study (Cragg 1979)

Table 1. Energy expenditure in *Podarcis lilfordi* from Nitge ($n = 11$, ± indicates standard error of mean)

Body mass (g)	Resting metabolism (kJ)			Metabolism during activity (kJ $\cdot$ dy^{-1})	Total FMR (kJ $\cdot$ dy^{-1})
	Day (12 h)	Night (12 h)	Total (day)		
5.129 ± 0.382	0.204	0.084	0.288	1.171 (5.74x)	1.255 ± 0.098 (4.36x)

Values are energy expenditures, in kJ, over the appropriate periods. Metabolism during activity (maintenance plus activity costs) and total field metabolic rates (FMR) are also expressed in relation to estimated maintenance costs during the activity period, and the entire day, respectively

(18 ants, 3 ant eggs, 4 Diptera, 2 insect larvae, 1 Isopod, 1 Homoptera, 1 Coleoptera and nine anthers).

Magnitude of body mass change (g $\cdot$ dy^{-1}) in recaptured animals was regressed (least-squares) onto body mass (logarithmic transformations, one outlier removed; $F_{1,9} = 11.50$, $P < 0.01$), rate of gain/loss in body mass in all 11 animals adjusted for the resultant regression equation to average body mass, and residual change (x = -0.00408 ± 0.00713 g $\cdot$ dy^{-1}) tested for deviation from zero. This indicated that there was no significant trend for either weight gain or loss in the population during the study period ($t_{10} = 0.570$, $P > 0.5$). Residual body mass change in labeled animals did not differ from that in two recaptured unlabeled animal ($F_{1,9} = 0.00$, $P > 0.95$).

Field metabolic rates

Mean CO_2 production in *P. lilfordi* was 2.034 ± 0.158 ml $\cdot$ CO_2 $\cdot$ h^{-1} ($n = 11$). FMR scaled on body mass with an exponent of 0.79 (Fig. 1), which does not differ from the interspecific exponent of 0.80 ($t_{10} = 0.14$, $P > 0.9$) determined for iguanid lizards (Nagy 1982). However, mean mass-specific FMR was 51.5% higher than that in the latter group (341.3 ± 18.0 J $\cdot$ g$^{-0.80}$ $\cdot$ day^{-1}; $t_{10} = 6.5$, $P < 0.001$). Although only two of the recaptured animals were females, making discrimination of between-sex differences difficult, no significant differences were found between male and female residuals ($F_{1,7} = 1.67$, $P > 0.2$) computed for the male FMR/body mass slope.

Maintenance and activity metabolism

Mean resting rates of oxygen consumption of captive *P. lilfordi* were 1.16 ml O_2 $\cdot$ h^{-1} at 33.5° C (x̄ body mass = 7.05 g, $n = 4$) and 0.47 ml O_2 $\cdot$ h^{-1} at 25° C (x̄ body mass = 7.27 g, $n = 4$) (see Table 1 for energy equivalents over estimated field-active and inactive periods). One 33.5° C and one 25° C recording were discarded because

intense sporadic activity within the chamber gave unstable oxygen consumption readings. Mean mass-specific values (33.5° C, 0.2541 ± 0.0064 ml $O_2 \cdot$ g$^{-0.779} \cdot$ h^{-1}; 25° C, 0.0993 ± 0.0068 ml $O_2 \cdot$ g$^{-0.779} \cdot$ h^{-1}) were determined using the exponent 0.779 – a mean of values determined from closely related species (Cragg 1978) – and extrapolated to each of the labeled animals. Resting maintenance energy expenditures were estimated for each lizard, based on the simplifying assumptions that they had been active every day, maintained preferred body temperatures (33.5° C) during the 12-h activity period, and remained at mean ambient shade temperatures (25° C) when inactive. Mean daily maintenance costs were 288.1 J $\cdot$ day^{-1}, representing 23% of total FMR (Table 1). Activity metabolism therefore accounted for the largest proportion of the FMR (77%) (Table 1). Activity metabolism constituted 82.6% of energy expenditure during the activity period.

Population density and energetics

No evidence was found of any other reptile species in Nitge. The population density of *P. lilfordi* was estimated at 12 190.0 ± 2135.5 ind $\cdot$ ha^{-1}. Mean individual FMRs were extrapolated to the rest of the population on the basis of body masses of all captured animals ($n = 64$, x̄ body mass = 4.615 g). Metabolizable energy demand for the population was calculated as 13.86 MJ $\cdot$ ha^{-1} $\cdot$ day^{-1}. Taking into account the errors associated with the density estimate and prediction of individual DEE gives a mean standard error of 3.20 MJ $\cdot$ day^{-1}. For comparison, the energy demand of a mammal population of the same body size and population density would be 141.6 MJ $\cdot$ ha^{-1} $\cdot$ day^{-1}, i.e., 10.2 times that for the *P. lilfordi* population (calculated from Nagy 1987).

Discussion

Population density and energetics

While densities of up to 10900 lizards $\cdot$ ha^{-1} have been reported for similar-sized *Anolis* lizards on islands in the

Caribbean (Andrews 1979), the population density estimate for *P. lilfordi* on Nitge appears to be one of the highest yet reported for a lizard population. The fact that it is the "only" terrestrial vertebrate (no evidence of geckos, rats or mice, was found although their presence cannot be ruled out; however three goats have been introduced) on Nitge must clearly play an important role in determining this.

Comparison with other population energetics studies emphasises the the extent of the contribution to the energy dynamics of the Nitge ecosystem made by this single species. For example, population metabolizable energy demand is 3.9 times higher than the estimated sum of 3.6 MJ · day^{-1} for three lizard species on the tropical Caribbean island of Bonaire (greatest demand by an individual species was 2.5 MJ · day^{-1} for *Cnemidophorus murinus*) (Bennett and Gorman 1979). This is primarily due to the high population biomass (56.3 kg · ha^{-1}, compared to 23.1 kg · ha^{-1} in Bonaire) but also the high individual FMR of *P. lilfordi*. While the latter island appears "continental" when compared with Nitge, i.e., it is much larger (250 km^2) and has greater species-richness (7 lizard species), true continental lizard populations show much lower energy demand due to lower population densities. A population of the iguanid *Sceloporus graciosus* (Utah, USA) has been shown to require about 0.03 MJ · day^{-1} (Congdon and Tinkle 1981), while a year-round study of *Uta stansburiana* (Nevada, USA) gave a metabolizable energy flow of 13.8 MJ · year^{-1} (Nagy 1983).

Based on prey data determined for the Kalahari lacertid *Eremias lugubris*, i.e., 78% water in insect prey containing 17.5 kJ · g^{-1} dry matter (Nagy et al. 1984), and an assimilation efficiency of 81% (Nagy 1982), the *P. lilfordi* population on Nitge would consume 1.27 kg insect · ha^{-1} · day^{-1} during the summer non-reproductive period if, on average, individuals were maintaining energy balance. This is equivalent to 13.5 kg insect · day^{-1} for the whole islet.

The precariously restricted distributions of many morphological well-differentiated forms of *P. lilfordi* which in some cases (as in the Nitge population) may be confined to a single tiny islet (Pérez-Mellado and Salvador 1988), means that this species is also of interest from a conservation perspective. If food availability provides a major constraint on population density, it is easy to envisage that the introduction of an endothermic insectivore, or a herbivore which indirectly reduced insect biomass through vegetation-loss (e.g., the introduction of more goats), could pose a serious threat to the survival of this population. For example, a population of insectivorous birds of 70 g body mass with a density of 144 ind · ha^{-1} would have approximately the same food requirements as *P. lilfordi* (calculated from Nagy 1987).

Individual field metabolism

On a mass-specific basis, summer FMR in *P. lilfordi* from Nitge is close to values reported for intensively foraging insectivorous lacertids and teiids which have the highest FMRs yet found in lizards. For example, values are 25% higher than in *Eremias lineoocellata* (273 J · g$^{-0.8}$ · day^{-1}), a lacertid from the Kalahari desert, but 23% and 5% lower, respectively, than the North American teiids *Cnemidophorus hyperythrus* (444 J · g$^{-0.8}$ · day^{-1}; Karasov and Anderson 1984) and *Cnemidophorus tigris* (360 J · g$^{-0.8}$ · day^{-1}; Anderson and Karasov 1981).

Despite the similar FMRs in *P. lilfordi* and *C. tigris* there are marked differences between the constituent maintenance and activity components. Maintenance metabolism accounts for a much smaller proportion of FMR in *P. lilfordi* (cf. 56 and 130 J · g^{-1} · day^{-1} respectively). Also, a comparison of the ratios of total energy expenditure during the activity period to resting metabolism at active body temperatures, indicates that "activity intensity" is 73% higher in *P. lilfordi* (cf. 5.7 and 3.3 times, respectively). A possible source of error associated with this estimate is the lack of quantified observations of activity periods in individual *P. lilfordi*. However, the 12 h·day^{-1} activity period is more likely to be an overestimate than an underestimate. If this is the case, resting costs may be lower than the estimated values, so energy expenditure due to activity may actually be underestimated.

In any event, the results clearly indicate intense activity in *P. lilfordi* throughout the activity period. Maximal oxygen consumption is around 8 times resting consumption in closely related lacertids (Cragg 1978), approximating to that in several other lizard species (Bennett and Dawson 1976). This suggests that *P. lilfordi* may be operating at around 75% of its maximum aerobic capacity during activity. Even greater activity expenditure has been reported for *Eremias lineoocellata* (12× resting; Nagy et al. 1984), and also reproductive female *Sceloporus virgatus* (8.3× resting; Merker and Nagy 1984). However, the shortness of the daily activity periods in these species (2.8 and 3.6 hrs · day^{-1}, respectively) means that activity accounts for a much smaller proportion of their daily respiratory metabolism compared to *P. lilfordi*.

Observations made by us suggest that the high activity metabolism results from intensive foraging rather than territorial defence. Stamps and Buechner (1985) have indicated that territorial defense is lowered in insular vertebrate populations living at high densities. Given the lack of significant body weight change in labeled animals, it does appear that they were harvesting enough food to meet energy costs. Hence, one hypothesis is that the extremely high population densities, combined with relatively poor trophic resources, could obligate intensive foraging throughout the day in order to maintain energy balance. This species has been observed to switch from insectivory to nectarivory – when *Chrithmum maritimum* flowers in late summer (Pérez-Mellado 1989). The uniqueness of this feeding strategy within the genus *Podarcis* further supports the hypothesis that trophic availability imposes major constraints on the time-energy budget of *P. lilfordi*.

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