

Does intraspecific variation in the energy value of a prey species to its predators matter in studies of ecological energetics? A case study using insectivorous vertebrates¹

Stephen J. BROOKS & Michael C. CALVER, School of Biological & Environmental Sciences, Murdoch University, Murdoch, Western Australia 6150, Australia, e-mail: calver@cleo.murdoch.edu.au

Christopher R. DICKMAN, School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia.

Catherine E. MEATHREL² & J. Stuart BRADLEY, School of Biological & Environmental Sciences, Murdoch University, Murdoch, Western Australia 6150, Australia.

Abstract: This study tested the assumption that variation in the energy value of different instars of a hemimetabolous insect makes no ecologically significant difference to rates of energy gain by its vertebrate predators and found it to be supported. Three mammal species, four bird species and a lizard species were used as predators and one grasshopper species as prey. Although instars of both male and female grasshoppers differed significantly in energy values, the energy returns to their predators based on these exact values were qualitatively similar to those produced when a commonly-used constant energy value of 23 J/mg dry weight was substituted. Regressions of specific energy returns on those based on the 23 J/mg constant were highly significant, so energy returns based on the constant were good predictors of those based on specific energy values. Although significant intraspecific variations in energy values occur in *Acrida conica* and probably in other hemimetabolous insects as well, the 23 J/mg dry weight constant appears adequate for most predation studies.

Keywords: grasshopper, predation, prey preference, handling time, energy value.

Résumé: Cette étude vérifie et vient appuyer l'hypothèse selon laquelle les différences dans la valeur énergétique selon les stades de développement d'un insecte hémimétabole n'engendre aucune différence significative au plan écologique dans les taux d'acquisition d'énergie par ses prédateurs vertébrés. Nous avons utilisé comme prédateurs, trois espèces de mammifères, quatre espèces d'oiseaux et une espèce de lézard, et comme proie, une espèce de sauterelles. Bien que la valeur énergétique des sauterelles mâles et femelles diffèrent de manière significative selon le stade de développement, les retours en énergie à leurs prédateurs, tout au moins sur la base des valeurs exactes, étaient similaires, au plan qualitatif, aux retours obtenus en substituant une valeur d'énergie constante de 23 J/mg de poids sec. Les valeurs de régression entre les retours en énergie par espèce et ceux obtenus sur la base de la constante de 23 J/mg sont très significatives, de sorte que les retours en énergie calculés avec cette constante permettent une bonne estimation des retours pour chaque espèce. Bien qu'il existe des différences intraspécifiques dans la valeur énergétique chez *Acrida conica* et probablement chez d'autres insectes hémimétaboles, il demeure néanmoins que la constante de 23 J/mg de poids sec semble appropriée pour la majorité des études de prédation.

Mots-clés: sauterelle, prédation, préférence pour une proie, durée de manipulation, valeur énergétique.

Introduction

Energy remains the most popular currency for use in optimal foraging models (Stephens & Krebs, 1986; Stephens, 1990). The cost-benefit function is the mathematically-determined relationship between diet choice and net rate of energy intake while the optimum is determined by identifying the diet that, subject to constraints, maximises the net rate of energy intake (Pyke, Pulliam & Charnov, 1977). It is, therefore, essential in studies of optimal foraging to determine the specific amount of energy a prey will return to a predator and the energetic costs of finding, subduing and consuming the prey.

Much research has concentrated on the important relationships between prey size and taxon on the one hand and predator search time, handling time and capture efficiency

on the other; predator taxa including invertebrates (Charnov, 1976; Nentwig, 1983), fish (Werner, 1974; Prejs, Lewandowski & Stanczykowska-Piotrowska, 1990), lizards (Pough, 1984; Diaz & Carrascal, 1993), birds (Davies, 1977; Sherry & McDade, 1982) and mammals (Calver, Bradley & King, 1988; Dickman, 1988) have been studied. Far fewer studies assess prey energy values. For example, the standard energy value of 23 J/mg dry weight proposed for insect prey by Golley (1961) and Cummins & Wuycheck (1971) is still widely accepted in studies of insectivory (Calver & Wooller, 1982; Savino, Marschall & Stein, 1992; Diaz & Carrascal, 1993; Hill & Grossman, 1993), and authors sometimes explicitly assume no seasonal or intraspecific variations in this value (Carpenter *et al.*, 1992). Are these assumptions valid? Golley (1961) cautioned that while conversions of biomass to energy using average energy values in the literature may be justifiable in extensive surveys, specific energy values should be determined if

¹Rec. 1995-09-11; acc. 1996-02-01.

²Present address: Department of Environmental Management and Ecology, La Trobe University, P.O. Box 821, Wodonga, Victoria 3690, Australia.

narrow, accurate studies are required. Since then, examples of considerable interspecific and intraspecific variation in energy values of insects have been reported by several authors including Bryant (1973), Redford & Dorea (1984) and Bell (1990), but the implications for insectivore diet selection are rarely explored. This is probably because both prey selection data and specific energetic data are time-consuming to collect in a single study. Nevertheless, it is crucial to know how important specific energy values are in studies of insectivory, or if the general energy value of 23 J/mg dry weight is adequate.

We approached this problem by using existing data on the body composition of the sexually dimorphic grasshopper *Acrida conica* Fabricius (Brooks, 1993; Calver *et al.*, 1994) to calculate energy values for the different instars of each sex. Specific energy values for each sex/instar combination determined by this approach were then combined with data on the handling times of five species of birds, three species of mammals and a lizard species attacking *A. conica* to determine the projected rate of energy gain of each predator feeding on a specific sex and instar of grasshopper. These figures were compared with those resulting if a constant value of 23 J/mg dry weight was used. Both specific energy values and those based on the constant gave very similar patterns of energy return across grasshopper instars for all predators.

Methods

Male *A. conica* have six instars, ranging in size from 11 mm long and 3 mg dry weight (first instar) to 40 mm long and 72 mg dry weight (adults), while females have seven instars, their lengths ranging from 11 mm to 58 mm, and their dry weights from 7.5 mg to 234.5 mg (Calver, 1985). Names, sample sizes and weights of the predators are given in Table I. All are known to eat grasshoppers (for the birds, Barker & Vestjens, 1989; for the mammals, Murray & Dickman, 1994 and Dickman, Predave & Downey, 1995; for the lizard, How, Dell & Wellington, 1986) and represent a wide range of insectivorous terrestrial vertebrates. Mammals and lizards were maintained in separate glass terraria under the conditions described in Fisher & Dickman (1993), the magpies, the butcherbirds and one magpie-lark were wild birds accustomed to soliciting food from people, while the other two magpie-larks, the wattlebird and the miners were in aviaries administered by either licensed wildlife caregivers or the Perth Zoological Gardens.

To determine the energy value of the grasshoppers to the predators, proportions (by dry weight) of lipid and protein in each sex/instar combination of juvenile *A. conica* were taken from Calver *et al.* (1994) and data for the adults from Brooks (1993). The energy values of grasshoppers were calculated using the constants of 23.7 J/mg of protein and 39.6 J/mg of lipid (Ricklefs, 1977; Bell, 1990), and assuming that 70% of this is metabolisable by birds (Ricklefs, 1974), 83% is metabolisable in mammals (Bell, 1990), and that lizards are intermediate at 75% efficiency (our guess).

To determine handling time for each predator species we aimed to record a minimum of three attacks by each individual on every prey instar/sex combination, although

TABLE I. Common names, scientific names, total numbers studied and body weights of the predators. Weights are taken from Dunning (1993) (birds), Strahan (1983) (mammals, except the recently named Lesser Hairy-footed Dunnart, where the value is the mean weight of our specimens) and How, Dell & Wellington (1986) (lizard). They are means of both males and females except for the red wattlebird (males only), the yellow-throated miner (only a range given, not a mean), and the brown antechinus where male and female weights are given

Common name	Scientific name	No.	Weight (g)
BIRDS			
Australian magpie	<i>Gymnorhina tibicen</i> Latham	3	314
Magpie-lark	<i>Grallina cyanoleuca</i> Latham	3	89
Yellow-throated miner	<i>Manorina flavigula</i> Gould	3	64-71
Grey butcherbird	<i>Cracticus torquatus</i> Latham	2	79
Red wattlebird	<i>Anthochaera carunculata</i> J. White	1	125
MAMMALS			
Brown antechinus	<i>Antechinus stuartii</i> Macleay	6	35M, 20F
Lesser hairy-footed dunnart	<i>Sminthopsis youngsoni</i> McKenzie & Archer	4	10
Spinifex hopping-mouse	<i>Notomys alexis</i> Thomas	6	35
LIZARD			
Spiny-tailed gecko	<i>Diplodactylus ciliaris</i> Boulenger	3	5

M = male; F = female.

this was not achieved in all cases because appropriate grasshopper prey had to be collected in the field and feeding regimes for captive animals had to fit the routines of the regular caregivers. Healthy, active grasshoppers were used in all trials. Hunger may influence handling time (Holling, 1966; Leyhausen, 1979), so we standardised predator hunger by feeding captive animals at the normal feeding time, and wild birds when they approached and solicited food. The mammals and lizards received no more than one prey per trial for grasshoppers weighing more than 1 g, or no more than 1 g of smaller prey in successive trials on the same day. Handling time was measured to the nearest second using a digital stopwatch, and taken from the moment the prey was seized until it was swallowed. No attempt was made to randomise the presentation of prey of different sizes, since grasshoppers were collected from the field and we were constrained by availability of both predators and prey at any given time. Overall, there was a tendency for predators to be fed smaller grasshoppers before larger ones.

Specific energy values for each sex and instar combination of prey were divided by handling times to obtain a gross rate of energy intake per minute for each predator species. Initially, for each predator species and grasshopper sex a two-way ANOVA with factors of individual predator and prey instar was performed to check for interaction between these effects. This could only be assessed in a proportion of cases because of empty cells where a particular individual predator had not attacked a specific prey instar, but in all cases where the analysis could be run the individual predator \times prey instar interactions were not significant even in the presence of highly significant main effects. In the absence of evidence of significant interactions, data for individuals within predator species were combined and the energy returns for each species preying on the different instars for male and female grasshoppers separately were

analysed with one-way ANOVA. These steps were then repeated using a constant 23 J/mg as the energy value of all grasshoppers, and the specific energy returns regressed against those based on the constant to determine if the constant-based returns were significant predictors of the specific energy returns.

Results

Energy values of male and female instars are shown in Table II. Analysis of variance revealed that both females and males varied significantly in energy value across the instars ($F_{6,218} = 13.31, p < 0.0001$, and $F_{5,153} = 13.56, p < 0.0001$, respectively). Female grasshoppers were most variable, with mean energy values ranging from a low of 23.38 J/mg dry weight for adults to a high of 29.65 J/mg dry weight for the first instar, while male mean energy values ranged from a low of 23.81 J/mg dry weight for adults to a high of 28.66 J/mg dry weight for the first instar.

TABLE II. Mean energy values for male and female grasshoppers (*Acrida conica*) from each instar. The sexes were analysed separately because of the extra instar in the females; within each sex, means that do not share a common superscript are significantly different (Scheffé test following one-way ANOVA, $p < 0.05$)

Instar	Energy value in kJ/mg dry weight ($\bar{x} \pm SE, n = \text{sample size}$)	
	Males	Females
1	28.66 \pm 0.75, $n = 4^a$	29.65 \pm 0.10, $n = 2^c$
2	27.39 \pm 1.05, $n = 13^a$	25.38 \pm 0.63, $n = 13^d$
3	23.16 \pm 0.23, $n = 20^b$	23.41 \pm 0.22, $n = 23^e$
4	24.26 \pm 0.34, $n = 34^b$	24.19 \pm 0.17, $n = 53^f$
5	24.07 \pm 0.23, $n = 54^b$	24.23 \pm 0.15, $n = 82^f$
6	23.81 \pm 0.23, $n = 34^b$	23.48 \pm 0.14, $n = 57^e$
7	no 7th instar in males	23.38 \pm 0.12, $n = 23^e$

The results of the one-way ANOVA tests for variation in energy return (treating specific energy values and those based on the 23 J/mg constant separately) for predators attacking different sexes and instars of grasshoppers are shown in Table III. There is almost perfect qualitative

TABLE III. Results of one-way ANOVA for the energy returns (based on both specific energy values for each instar and the constant 23 J/mg) from male and female prey of each predator, as shown in Figure 1

Predator	Prey sex	Returns based on 23 J/mg constant		Returns based on specific energy values	
		F	p	F	p
Spinifex hopping-mouse	Male	$F_{(5,33)} = 9.60$	$p < 0.01$	$F_{(5,33)} = 8.66$	$p < 0.01$
	Female	$F_{(6,39)} = 10.50$	$p < 0.01$	$F_{(6,39)} = 7.76$	$p < 0.01$
Brown antechinus	Male	$F_{(5,43)} = 20.96$	$p < 0.01$	$F_{(5,43)} = 18.71$	$p < 0.01$
	Female	$F_{(6,32)} = 12.95$	$p < 0.01$	$F_{(6,32)} = 10.85$	$p < 0.01$
Lesser hairy-footed dunnart	Male	$F_{(5,20)} = 6.98$	$p < 0.01$	$F_{(5,20)} = 5.57$	$p < 0.01$
	Female	$F_{(6,39)} = 2.171$	$p = 0.083$	$F_{(6,39)} = 3.96$	$p < 0.001$
Australian magpie	Male	$F_{(4,102)} = 13.45$	$p < 0.01$	$F_{(4,102)} = 13.32$	$p < 0.01$
	Female	$F_{(6,110)} = 9.79$	$p < 0.01$	$F_{(6,110)} = 9.66$	$p < 0.01$
Magpie-lark	Male	$F_{(5,82)} = 6.02$	$p < 0.01$	$F_{(5,82)} = 5.65$	$p < 0.01$
	Female	$F_{(6,99)} = 6.32$	$p < 0.01$	$F_{(6,99)} = 6.22$	$p < 0.01$
Grey butcherbird	Male	$F_{(5,54)} = 7.86$	$p < 0.01$	$F_{(5,54)} = 7.31$	$p < 0.01$
	Female	$F_{(6,56)} = 2.93$	$p < 0.05$	$F_{(6,56)} = 2.67$	$p < 0.05$
Red wattlebird	Male	$F_{(5,9)} = 4.50$	$p < 0.025$	$F_{(5,9)} = 4.38$	$p < 0.05$
	Female	$F_{(5,20)} = 1.82$	$p = 0.154$	$F_{(5,20)} = 1.69$	$p = 0.182$
Yellow-throated miner	Male	$F_{(5,81)} = 2.24$	$p = 0.058$	$F_{(5,81)} = 2.79$	$p < 0.05$
	Female	$F_{(5,73)} = 6.82$	$p < 0.01$	$F_{(5,73)} = 6.91$	$p < 0.01$
Spiny-tailed gecko	Male	$F_{(5,14)} = 3.74$	$p < 0.05$	$F_{(5,14)} = 3.93$	$p < 0.05$
	Female	$F_{(5,19)} = 5.11$	$p < 0.01$	$F_{(5,19)} = 5.78$	$p < 0.04$

agreement between the conclusions reached based on both methods of determining energy return. The only exceptions were the yellow-throated miner attacking male prey and the lesser hairy-footed dunnart attacking female prey (no significant difference between prey instars occurring with constant-based energy returns, while specific energy values showed a significant difference).

The relationships between net energy gain (when using a standard value of 23 J/mg dry weight and when using specific energy values) prey instar, and prey sex are shown in Figure 1. By inspection, the two plots are extremely similar. In general, the maximum rate of energy intake was related to predator size, with larger predators capable of gaining more energy per unit time than smaller predators.

Regressions of specific energy returns on constant-based energy returns were significant at $p = 0.002$ or better for all predator species \times prey sex combinations, all r^2 values exceeded 0.92, and slopes for the regressions were all close to 1 (range 0.98 - 1.29). This indicates that calculations based on the 23 J/mg constant were good predictors of the results determined from specific energy values and supports the subjective conclusion reached by inspection alone.

Discussion

The range of energy values for all instars in both sexes closely approximated the standard value of 23 J/mg dry weight proposed by Golley (1961) and Cummins & Wuycheck (1971), although there were significant energy differences between instars in both sexes. However, these differences did not translate into markedly different patterns of energy returns for the predators, or different ecological interpretations of the results.

It appears that the more specific energy values are not critical in reaching general conclusions, despite the fact that they reveal significant differences amongst the instars of each sex. Of course, *A. conica* is only one species of hemimetabolous terrestrial insect, and much greater variations in

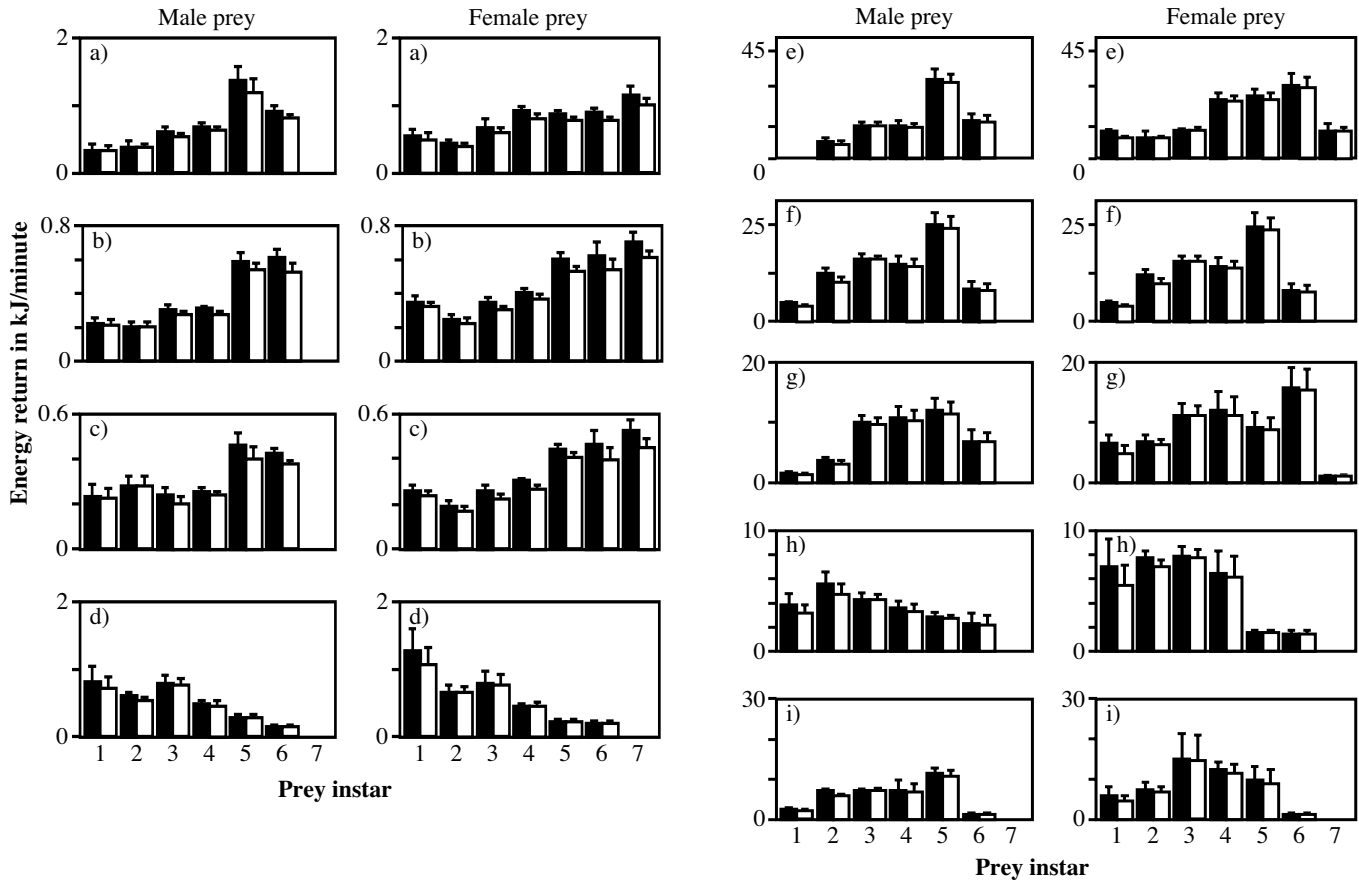


FIGURE 1. Energy returns in kJ/minute for predators feeding on different instars of male and female grasshoppers. Means are shown with standard errors. Shaded bars indicate energy returns computed on the basis of specific energy values for each sex and instar of grasshopper (Table I), while unshaded bars indicate energy returns calculated on the basis of a constant value of 23 J/mg dry weight for all stages in both sexes. For mammalian predators are: a) spinifex hopping-mouse (*Notomys alexis* Thomas), b) brown antechinus (*Antechinus stuartii* Macleay), c) lesser hairy-footed dunnart (*Sminthopsis youngsoni* McKenzie and Archer); the reptilian predator is: d) spiny-tailed gecko (*Diplodactylus ciliaris* Boulenger); and the avian predators are: e) Australian magpie (*Gymnorhina tibicen* Latham), f) magpie-lark (*Grallina cyanoleuca* Latham), g) grey butcherbird (*Cracticus torquatus* Latham), h) yellow-throated miner (*Manorina flavigula* Gould), and i) red wattlebird (*Anthochaera carunculata* J. White).

energy content could occur within other species from other environments. Redford & Dorea (1984) and Bell (1990) generalised from a survey of the literature that adult insects do not vary greatly in organic nutritional content, and we concur with this conclusion. Nevertheless, they found also that the larval and pupal forms of holometabolous insects were high in lipid and hence offered large nutritional rewards, a feature which should taken into account in foraging studies. Whilst those studying the immature stages of holometabolous insects may wish to incorporate precise energy values for the different stages into their calculations, studies involving nymphs and adults of hemimetabolous insect prey are likely to be safe in using the standard energy return figure. However, similar generalisations cannot be made for the mineral nutrient composition of insects, since Keeler & Studier (1992) and Studier, Keeler & Sevicik (1991) have highlighted intraspecific differences in the mineral nutrient composition that might need to be included as constraints in optimal foraging models.

Acknowledgements

We thank D. Miller, curator at the Perth Zoological Gardens, for permission to study birds in his collection, and the bird keepers

for valuable assistance. K. Pryce-Howells, B. Porter, and staff of the Brand Wildlife Centre, Malaga, kindly allowed us access to birds in their care. The work was supported in part by a Murdoch University Special Research Grant (Calver), and a grant from the Australian Research Council (Dickman).

Literature cited

Barker, R. D. & W. J. M. Vestjens, 1989. The Food of Australian Birds. II Passerines. CSIRO Division of Wildlife and Ecology, Lyneham Australian Capital Territory, Canberra.

Bell, G. P., 1990. Birds and mammals on an insect diet: A primer on diet composition analysis in relation to ecological energetics. *Studies in Avian Biology*, 13: 416-422.

Brooks, S. J., 1993. The nutrient composition of the instars and colour morphs of male and female grasshoppers (*Acrida conica*) and its applicability to the optimal foraging theorem. Honours thesis, School of Biological and Environmental Sciences, Murdoch University, Murdoch, Western Australia.

Bryant, D. M., 1973. The factors influencing the selection of food by the House Martin (*Delichon urbica* L.). *Journal of Animal Ecology*, 42: 539-564.

Calver, M. C., 1985. Some aspects of the population biology of the grasshopper *Acrida conica* Fabricius. Ph.D. thesis, School of Biological and Environmental Sciences, Murdoch University,

- Murdoch, Western Australia.
- Calver, M. C. & R. D. Wooller, 1982. A technique for assessing the taxa, length, dry weight and energy content of the arthropod prey of birds. *Australian Wildlife Research*, 9: 293-301.
- Calver, M. C., J. S. Bradley & D. R. King, 1988. The relationship between prey size and handling time and prey size and capture success in three sympatric species of dasyurid marsupials. *Australian Wildlife Research*, 15: 615-623.
- Calver, M. C., S. J. Brooks, J. S. Bradley & I. W. Wright, 1994. Ecological and physiological correlates of microhabitat selection in the grasshopper *Acrida conica* Fabricius. *Entomology - Trends in Agricultural Sciences*, 2: 95-106
- Carpenter, S. K., C. E. Kraft, R. Wright, Xi He, P. A. Soranno & J. R. Hodgson, 1992. Resilience and resistance of a lake phosphorous cycle before and after food web manipulation. *American Naturalist*, 140: 781-798.
- Charnov, E. L., 1976. Optimal foraging: Attack strategy of a mantid. *American Naturalist*, 110: 141-151.
- Cummins, J. W. & J. C. Wuycheck, 1971. Caloric equivalents for investigation in ecological energetics. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 18: 1-158.
- Davies, N. B., 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*): A field study on optimal foraging. *Animal Behaviour*, 28: 1016-1033.
- Diaz, J. A. & L. M. Carrascal, 1993. Variation in the effect of profitability on prey size selection by the lacertid lizard *Psammodromus algirus*. *Oecologia*, 94: 23-29.
- Dickman, C. R., 1988. Body size, prey size and community structure in insectivorous mammals. *Ecology*, 69: 569-580.
- Dickman, C. R., M. Predavec & F. J. Downey, 1995. Long-range movements of small mammals in arid Australia: Implications for land management. *Journal of Arid Environments*, 31: 444-452.
- Dunning, J. B. Jr., 1993. (ed.) *CRC Handbook of Avian Body Masses*. CRC Press, London.
- Fisher, D. O. & C. R. Dickman, 1993. Body size-prey size relationships in insectivorous marsupials: Tests of three hypotheses. *Ecology*, 74: 1871-1883.
- Golley, F. B., 1961. Energy values of ecological materials. *Ecology*, 42: 581-584.
- Hill, J. & G. D. Grossman, 1993. An energetic model of microhabitat use for rainbow trout and rosieside dace. *Ecology*, 74: 685-698.
- Holling, C. S., 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada*, 48: 1-86.
- How, R. A., J. Dell & B. D. Wellington, 1986. Comparative biology of eight species of *Diplodactylus* gecko in Western Australia. *Herpetologica*, 42: 471-482.
- Keeler, J. O. & E. H. Studier, 1992. Nutrition in pregnant big brown bats (*Eptesicus fuscus*) feeding on June beetles. *Journal of Mammalogy*, 73: 426-430.
- Leyhausen, P., 1979. *Cat Behaviour: The Predatory and Social Behaviour of Domestic and Wild Cats*. Garland STPM Press, New York.
- Murray, B. R. & C. R. Dickman, 1994. Granivory and microhabitat use in Australian desert rodents: Are seeds important? *Oecologia*, 99: 216-225.
- Nentwig, W., 1983. The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linphyiidae, Pholcidae, Agelenidae). *Oecologia*, 56: 132-139.
- Pough, F. H., 1984. The advantage of ectothermy for tetrapods. *American Naturalist*, 115: 92-112.
- Pough, F. H. & R. M. Andrews, 1985. Energy costs of subduing and swallowing prey for a lizard. *Ecology*, 66: 1829-1836.
- Prejs, A., K. Lewandowski & A. Stanczykowska-Piotrowska, 1990. Size-selective predation by roach (*Rutilus rutilus*) on zebra mussel (*Dreissena polymorpha*): field studies. *Oecologia*, 83: 378-384.
- Pyke, G. H., H. R. Pulliam & E. L. Charnov, 1977. Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology*, 52: 137-154.
- Redford, K. H. & J. G. Dorea, 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *Journal of Zoology*, 203: 385-395.
- Ricklefs, R. E., 1974. Ecological aspects of avian energetics. Pages 152-297 in R. A. Paynter (ed.). *Avian Energetics*. Nuttall Ornithological Club, Cambridge, Massachusetts.
- Ricklefs, R. E., 1977. Composition of eggs of several bird species. *Auk*, 94: 350-356.
- Savino, J. F., E. A. Marschall & R. A. Stein, 1992. Bluegill growth as modified by plant density: An exploration of underlying mechanisms. *Oecologia*, 89: 153-160.
- Sherry, T. W. & L. A. McDade, 1982. Prey selection and handling in two neotropical hover-gleaning birds. *Ecology*, 63: 1016-1028.
- Stephens, D. W., 1990. Foraging theory: Up, down and sideways. *Studies in Avian Biology*, 13: 444-454.
- Stephens, D. W. & J. R. Krebs, 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Strahan, R. (ed.), 1983. *Complete book of Australian Mammals*. Angus & Robertson, London.
- Studier, E. H., J. O. Keeler & S. H. Sevick, 1991. Nutrient composition of caterpillars, pupae and adults of the eastern tent moth, (*Malacosoma americanum*) Lepidoptera: Lasicampidae. *Comparative Biochemistry and Physiology*, 100A: 1041-1043.
- Werner, E. F., 1974. The fish size, prey size, handling time relation in several sun fishes and some implications. *Journal of the Fisheries Research Board of Canada*, 31: 1531-1536.