

A first approximation of the energetics of Cape sugarbirds (*Promerops cafer*) and orange-breasted sunbirds (*Nectarinia violacea*)

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Estimated expenditures by *Nectarinia violacea* and *Promerops cafer* vary throughout the day, with highest rates occurring during the morning when nectar availability is greatest. Energy storage needed to satisfy overnight requirements by these nectarivores probably occurs only during the morning, with deficits being incurred at other times, although the ingestion of insects may help to reduce these deficits. Male and female *P. cafer* are frequently territorial, showing a clear preference for foraging at partially opened inflorescences of *Mimetus hirtus*. Smaller male *N. violacea* are usually excluded from *M. hirtus* and obliged to forage on less rewarding *Erica perspicua*.

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Geskatte energieverbruik deur *Nectarinia violacea* en *Promerops cafer* wissel deur die dag met die hoogste tempos gedurende die oggend as die nektarbeskikbaarheid die hoogste is. Energieberging om in die oornagbenodighede van hierdie nektarivore te voorsien vind waarskynlik slegs in die oggend plaas terwyl tekorte op ander tye plaasvind, alhoewel die inname van insekte mag bydra om hierdie tekorte te verminder. Manlike en vroulike *P. cafer* is dikwels territoriaal, en toon 'n duidelike voorkeur om te voed by gedeeltelike oop blomme van *Mimetus hirtus*. Die kleiner manlike *N. violacea* word gewoonlik van *M. hirtus* weggehou en is genoodsaak om die minder lonende *Erica perspicua* te gebruik.

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The energetics and foraging behaviour of avian nectarivores have been studied intensively in recent years. In some instances, time and energy budgets have been established for birds maintained under laboratory conditions (e.g. Hainsworth, Collins & Wolf 1977; Collins & Clow 1978; Collins & Morellini 1979; Hainsworth & Wolf 1979; Collins, Cary & Packard 1980; Collins & Briffa 1983a). In other cases, investigators have examined ways in which energy and time are partitioned by nectarivores in the field (e.g. Wolf & Hainsworth 1971; Gill & Wolf 1975; Wolf 1975; Wolf, Hainsworth & Gill 1975; Frost & Frost 1980; Ford 1981; Collins & Briffa 1983b).

Most attention has been devoted to the energetics of American hummingbirds and Australian honeyeaters, although several studies have involved sunbird species extant in East Africa (e.g. Gill & Wolf 1975; Wolf 1975). Few attempts have been made, however, to quantify energy flux or foraging behaviour for nectarivores in southern Africa, apart from preliminary studies of energy requirements and factors underlying nest site selection by the Cape sugarbird (Burger, Siegfried & Frost 1976; Mostert, Siegfried & Louw 1980), and resource utilization by sunbirds visiting *Leonotis leonurus* (Frost & Frost 1980).

The purpose of the present study was to help remedy this deficiency by documenting diurnal variations in energy expenditure and intake by two co-occurring nectarivores in the southwest Cape, the Cape sugarbird (*Promerops cafer*) and the orange-breasted sunbird (*Nectarinia violacea*). Attention was also paid to the manner in which available nectar energy was partitioned between the two nectarivore species. The study involved a small number of birds, over a relatively short period of time, and was intended as a precursor to more comprehensive investigations.

Materials and Methods

Study site and experimental design

Investigations were conducted at Betty's Bay, approximately 90 km south-east of Cape Town on the south coast, during September 1982. The study site was situated on a narrow belt of coastal seepage fynbos, where *Mimetus hirtus* (Proteaceae) and *Erica perspicua* (Ericaceae) were the major plant species in flower at that time (Collins 1983). These plants tend to occur in separate habitats, with only a slight overlap in their geographical distributions. *M. hirtus* is approximately 1.5 m high, with numerous terminal flowering heads that each bear several inflorescences. As described elsewhere (Collins 1983), each inflorescence comprises 8 to 11 florets, all of which eventually produce erect styles and pollen presenters. Inflorescences

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in which only some of the styles are erect have been classified as being 'partially open', those where all styles are erect as 'fully open'. *E. perspicua* is generally shorter and less robust than *M. hirtus*, with a relatively large number of individual flowers borne on each flowering head. These flowers are either closed or fully open.

The principal nectarivores at Betty's Bay were *Promerops cafer* and *Nectarinia violacea*. Several individual male and female *P. cafer* defended small non-breeding territories within stands of *M. hirtus*. Others appeared to range over much greater areas and be non-territorial, although none were ever observed foraging on *E. perspicua*. It was not possible to determine whether *N. violacea* was territorial, although members of this species were usually associated with habitats in which *E. perspicua* was dominant. Attempts by *N. violacea* to forage in *M. hirtus* were frequently frustrated by territorial *P. cafer*.

Two observation stations were established at the study site. One was located near the junction of territories occupied by single colour-banded male and female *P. cafer*, and the other next to a nearby patch of *E. perspicua*. Foraging activity was observed, and time-budget data recorded, for the two *P. cafer* and several male *N. violacea*, over a period of several days. Female *N. violacea* were not studied, as they were rare and difficult to observe against the background vegetation. Nectar standing crop volumes and concentrations were measured for the dominant plant species at each station, as were air temperatures within the vegetation. Field data were subsequently integrated with estimated unit energy costs of various activities to predict diurnal variations in total energy expenditure and intake for individual *P. cafer* and *N. violacea*.

Foraging behaviour

The colour-banded territorial female *P. cafer* was observed for at least 15 min during each hour of daylight over two consecutive days. During each interval, the total number of *M. hirtus* inflorescences probed by the bird was recorded. Similar observations were made for the banded male *P. cafer* and several male *N. violacea* on a subsequent day. As it proved impossible to follow individual *N. violacea* for more than 1–2 min, foraging data for several birds were pooled.

Nectar energy availability

Nectar standing crop volumes in randomly selected partially and fully opened *M. hirtus* inflorescences were measured at 06h30, 10h30, 13h30 and 17h30 on two successive days, using 5 μ l capillary tubes. Volumes present in open *E. perspicua* flowers were measured at similar times. Different inflorescences (flowers) were sampled on each occasion. When sufficient nectar was present, equivalent sucrose concentrations (mg sucrose/100 mg nectar) were estimated using a temperature-compensated refractometer (Collins & Briffa 1982; Collins 1983).

Several previous studies have shown that sucrose, glucose and fructose constitute almost all of the solute present in nectar collected from a wide range of plants, with sucrose usually the predominant carbohydrate (e.g. Baker 1975; Wiens, Rourke, Casper, Rickart, La Pine & Petersen 1982). The refractive index measured was influenced by all solutes present, although the refractometer was calibrated to give the concentration of a sucrose solution that would have a refractive index identical to that of the nectar (Wolf & Hainsworth 1971). Energy equivalents of standing crop volumes were predicted assuming that 1 mg sucrose represents 16.74 J (Collins & Briffa 1983a). Validation experiments have suggested that energy

values predicted in this way may be approximately 2% higher than those obtained if bomb calorimetry of samples was performed (Collins, unpublished data).

Nectarivore time and energy budgets

Rates of nectar energy uptake by birds were estimated at 06h30, 10h30, 13h30 and 17h30, using the formula:

$$\text{kJ/h} = \text{probes/s} \times \mu\text{l nectar} \times \text{mg sucrose}/100 \mu\text{l nectar} \times 0,036$$

Appropriate probing rates and nectar standing crop volumes were substituted in this formula, assuming that all standing crop nectar was drained from a flower or inflorescence each time it was probed by a bird. Estimates of mg sucrose/100 μ l nectar were derived from measured nectar concentrations, using appropriate conversion tables provided in Weast (1975).

Digital stopwatches were used to record the amounts of time devoted to flight and non-flight activity by nectarivores at intervals throughout the day. In general, time-budget data were collected simultaneously with the recording of floral probing rates. Non-flight activity incorporated resting, calling, preening and probing, and is referred to subsequently as perching. Flight included all airborne activity such as long- and short-distance flight, and hopping (Collins & Briffa 1983b).

Time-budget data gathered during the day were converted to estimates of energy expenditure using the method summarized in Figure 1. Body masses for *P. cafer* were derived from actual values for banded birds caught in mist nets during the study period, assuming linear mass increases of 0.6 g throughout the day. As individual male *N. violacea* could not be followed for extended periods, masses used were based on the mean value for 10 birds, assuming a diurnal increase of 0.4 g (Cheke 1971; Collins 1981). Temperatures used in calculations were those recorded every hour by means of unshielded thermistors, placed in vegetation visited by nectarivores and connected to a multi-channel telethermometer (Collins & Briffa 1983b). It was assumed that body temperatures (T_B) and lower critical temperatures (T_{LC}) were similar to those of other nectarivorous passerines such as honeyeaters (Collins, Cary &

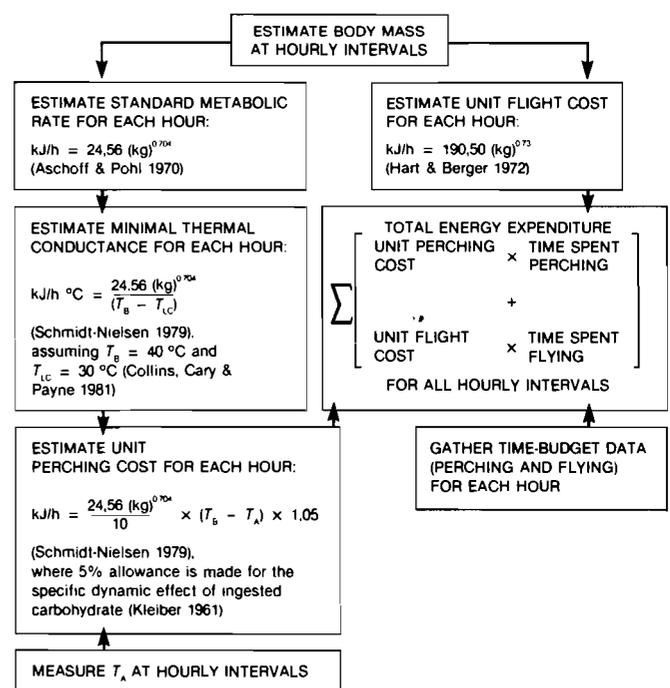


Figure 1 Steps involved in the calculation of total diurnal energy expenditures by nectarivorous passerines.

Payne 1981), and that conductance remained constant at environmental temperatures (T_A) below the T_{LC} .

Night-time energy expenditures were estimated in a similar fashion to that indicated in Figure 1. The major differences were that uniform nocturnal mass losses equivalent to daytime gains were assumed, no allowance for flight or the influence of ingested food was necessary, and different equations were used to predict unit perching costs:

$$\text{kJ/h} = \frac{20,01 (\text{kg})^{0,726}}{37-25} \times (37 - T_A)$$

(Aschoff & Pohl 1970; Schmidt-Nielsen 1979; Collins, Cary & Payne 1981.) Predicted unit perching costs were significantly lower than values estimated at equivalent temperatures during the day. Similar differences have been shown for costs based on a limited number of direct measurements of oxygen consumption for *N. violacea* (Collins, unpublished data).

Total energy requirements were predicted in the manner described by Collins & Briffa (1983b). It was assumed that birds ingested sufficient energy during the day to satisfy their immediate requirements, plus those incurred during the following night. Total assimilation of ingested carbohydrate, and 12,5% loss of energy when excess carbohydrate was stored as lipid, were also assumed (Collins, Cary & Packard 1980; Collins & Briffa 1983a).

Results

Foraging and general behaviour

The female *Promerops cafer* studied spent considerable time sheltering in *Mimetes hirtus* bushes near the centre of its non-breeding territory. It rarely moved from there except to forage or chase intruders. The male *P. cafer* also defended a similar-sized territory, but tended to perch on top of elevated flowering heads. This bird occasionally left its territory for short intervals, sometimes being seen to travel over distances of more than 500 m. Neither of the two birds was observed foraging for nectar on plants other than *M. hirtus*. Hourly variations

in the rates at which birds probed inflorescences within their territories are shown in Figure 2. The female bird tended to probe less frequently shortly after dawn and around midday than at other times. In contrast, the male probed at a generally faster and more consistent rate throughout the day ($\bar{X} \pm \text{SD}$ for entire day: male $0,072 \pm 0,030$ probes/s on 21 Sept.; female $0,046 \pm 0,036$ probes/s on 19 Sept.; female $0,035 \pm 0,019$ probes/s on 20 Sept.).

Male *N. violacea* were generally more mobile than *P. cafer*. They occasionally visited *M. hirtus* inflorescences, although probing rates were not measured. Limited data available for such birds visiting *E. perspicua*, however, suggest that probing rates were higher than for *P. cafer* at *M. hirtus* (Figure 2).

Nectar energy availability

Nectar standing crop volumes for partially opened *M. hirtus*

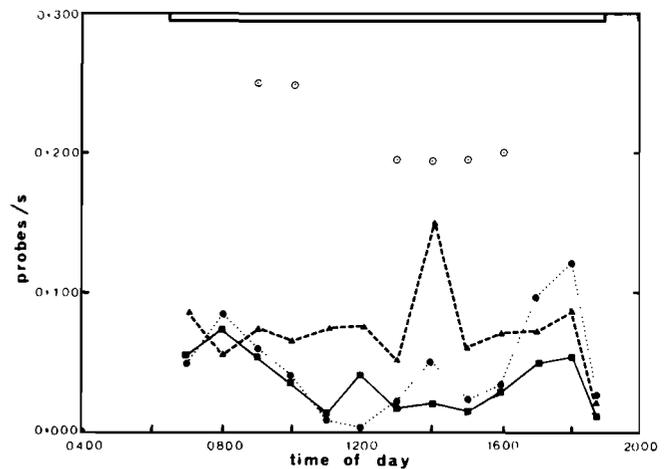


Figure 2 Temporal variations in the rates at which a territorial female *P. cafer* (● 19 September; ■ 20 September), and a territorial male *P. cafer* (▲ 22 September), probe *M. hirtus* inflorescences. Some rates at which male *N. violacea* (⊙ 22 September) probe *E. perspicua* flowers are also shown. Duration of the photoperiod is indicated by the horizontal box.

Table 1 Nectar standing crop volumes, equivalent sucrose concentrations and energy values for *M. hirtus* and *E. perspicua*

Date and time of day	Plant species					
	<i>Erica perspicua</i> ^a			<i>Mimetes hirtus</i> ^b		
	μl nectar/ flower	mg sucrose/ 100 μl nectar	mean energy content (J)	μl nectar/ inflor.	mg sucrose/ 100 μl nectar	mean energy content (J)
19 September						
06h30	0,9 ± 2,0	25,2 ± 0,7	3,8	40,0 ± 24,1	15,6 ± 0,9	104,5
10h30	0,3 ± 0,7	...	1,3	28,0 ± 18,2	...	73,1
13h30	0,5 ± 1,2	...	2,1	2,0 ± 3,1	...	5,2
17h30	0,3 ± 0,7	...	1,3	5,4 ± 9,1	...	14,1
20 September						
06h30	0,6 ± 2,1	24,8 ± 0,9	2,5	46,1 ± 45,3 (8,0 ± 22,0)	15,4 ± 1,2	118,8 (20,6)
10h30	0,5 ± 0,9	...	2,0	2,5 ± 3,7 (2,3 ± 2,6)	...	6,4 (5,9)
13h30	0,8 ± 1,5	...	3,0	2,1 ± 1,1 (11,8 ± 22,8)	...	5,4 (30,4)
17h30	0,5 ± 0,7	...	2,1	8,0 ± 8,3 (1,3 ± 2,3)	...	20,6 (3,4)

^aVolumes were obtained for 50 *E. perspicua* flowers on each occasion, although concentrations were measured for only 20. Calculations assume that nectar concentration does not vary with time of day.

^bSample size was 10 for *M. hirtus* on each occasion; values in parentheses are $\bar{x} \pm \text{SD}$ for fully opened inflorescences, other values are for partially opened inflorescences.

inflorescences generally decreased significantly after 06h30, although not between 06h30 and 10h30 on 19 September, with a slight recovery late in the day (Table 1; $P \leq 0,05$ at least for 5 of 6 possible *t*-test comparisons with 06h30-values). Volumes for fully opened inflorescences did not vary in this way, and were statistically indistinguishable from equivalent values for partially opened inflorescences, except at 06h30 and 17h30 ($P \leq 0,05$ at both times). *E. perspicua* flowers showed no significant change in nectar availability throughout the day.

Equivalent sucrose concentrations for *M. hirtus* nectar were significantly less than those for *E. perspicua* ($P \leq 0,001$). Nevertheless, standing crop nectar energy availability is generally much greater in *M. hirtus* inflorescences, with most energy being available early in the day in partially opened inflorescences (Table 1).

Time and energy budgets

Variations in environmental temperature, and time- and

energy-budget estimates for the territorial female *P. cafer*, are illustrated in Figure 3. The time devoted to flight, and total energy expended, both decrease during the middle of the day. At night, there is no flight and the general level of metabolic activity is low. Similar overall trends were shown by the territorial male *P. cafer* and by male *N. violacea*, although the latter appeared to fly for a significantly greater proportion of the day than either of the *P. cafer* (Table 2). Male *N. violacea* require considerably less energy than the other birds in order to satisfy their total daily energy needs, although their mean mass-relative requirement (5 313 kJ/kg) is greater than that of the two *P. cafer* (3 243 kJ/kg).

Hourly variations in energy expenditure by all nectarivores studied are indicated in Table 3. Estimates of possible nectar energy intake are also shown, for periods when nectar standing crop volumes and probing rates were measured. Standing crop nectar energy equivalents for partially open *M. hirtus* inflorescences have been used in calculations, in view of the ob-

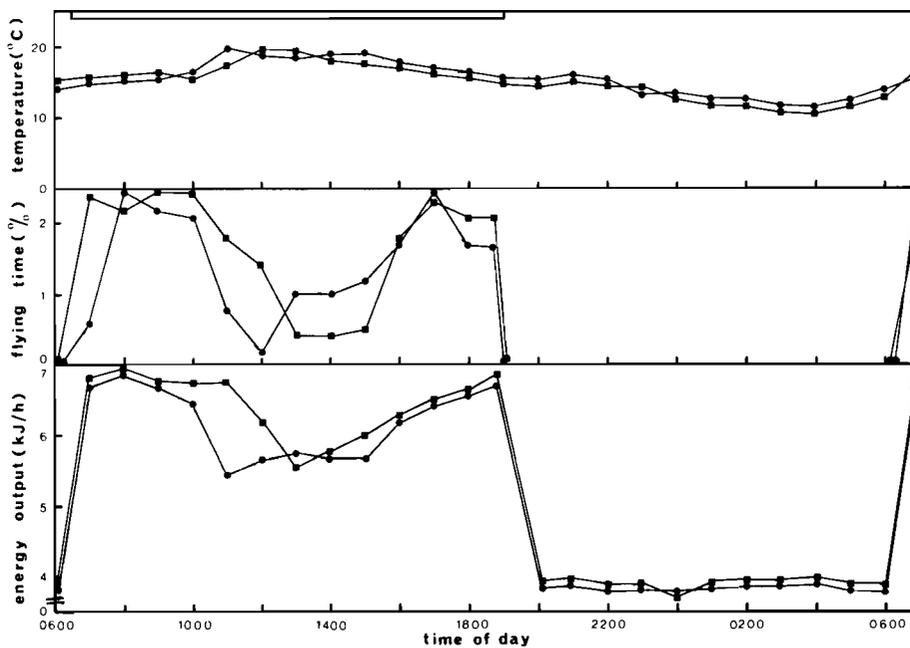


Figure 3 Diurnal variations in environmental temperature, and time and energy budgets for a territorial female *P. cafer* exposed to these temperatures (● 19–20 September; ■ 20–21 September). Duration of the photoperiod is indicated as in Figure 2.

Table 2 Time and energy-budget data for *P. cafer* and *N. violacea*

Bird species and date	Mean body mass (g) ^a	Mean day/night temp. (°C)	Mean time spent flying during day (%)	Daytime energy expenditure (kJ)	Night-time energy expenditure (kJ)	Required energy acquisition during day (kJ)
19–20 September						
Female <i>P. cafer</i> (R/y)	40,5	17,6/13,5	1,5 (13,1 × 10 ³) ^b	77,7	43,9	128,0
20–21 September						
Female <i>P. cafer</i> (R/y)	40,5	16,8/13,0	1,7 (15,3 × 10 ³)	80,5	44,9	131,8
22–23 September						
Male <i>P. cafer</i>	41,8	17,7/12,5	5,2 (3,6 × 10 ³)	84,9	46,9	138,5
Male <i>N. violacea</i>	9,9	17,7/12,5	11,0 (3,8 × 10 ³)	33,8	16,5	52,6

^aMean body mass for *N. violacea* is based on measurements for 10 birds; means for male and female *P. cafer* were obtained from measurements for colour-banded birds on the day prior to and the day following time-budget measurements.

^bFigures in parentheses indicate approximate total times (s) spent gathering time-budget data. Single *P. cafer* were studied throughout each day (the same bird on 19–20 and 20–21 September), although data for *N. violacea* are a composite for several birds.

Table 3 Temporal changes in estimated energy uptake and expenditure by *P. cafer* and *N. violacea*

Time of day	Bird species							
	Female <i>P. cafer</i> (19 Sept.) ^a		Female <i>P. cafer</i> (20 Sept.) ^a		Male <i>P. cafer</i> (22 Sept.) ^a		Male <i>N. violacea</i> (22 Sept.) ^b	
	energy uptake (kJ)	energy expend. (kJ)	energy uptake (kJ)	energy expend. (kJ)	energy uptake (kJ)	energy expend. (kJ)	energy uptake (kJ)	energy expend. (kJ)
06h30–07h30	18,82	6,73	22,24	6,84	36,78	8,40	2,95	2,84
07h30–08h30	...	6,94	...	6,90	...	7,37	...	2,74
08h30–09h30	...	6,68	...	6,77	...	6,84	...	2,87
09h30–10h30	...	6,46	...	6,76	...	6,43	...	2,85
10h30–11h30	2,63	5,47	0,30	6,77	1,78	6,28	0,98	2,57
11h30–12h30	...	5,69	...	6,22	...	6,07	...	2,45
12h30–13h30	...	5,77	...	5,64	...	6,07	...	2,54
13h30–14h30	0,94	5,74	0,43	5,72	2,90	6,49	1,64	2,61
14h30–15h30	...	5,71	...	6,00	...	6,09	...	2,59
15h30–16h30	...	6,17	...	6,32	...	7,02	...	2,51
16h30–17h30	...	6,46	...	6,48	...	7,35	...	3,02
17h30–18h30	6,24	6,57	4,00	6,67	6,45	6,85	0,98	2,78
18h30–19h00	...	3,34	...	3,46	...	3,65	...	1,46
Total		77,74		80,52		84,91		33,77

^aEstimates of energy uptake by female *P. cafer* were based on probing rates and nectar volumes for partially opened *M. hirtus* inflorescences measured on those days; estimates for male *P. cafer* used volumes measured on 20 September.

^bPredictions for *N. violacea* assumed a constant probing rate of 0,216 probes/s, and used nectar volumes for *E. perspicua* on 19 September.

vious preference for these inflorescences shown by *P. cafer* (Collins 1983). It appears as if nectar energy intake by *P. cafer* only exceeds expenditure early in the day, although continued survival of birds implies that total daily energy intake must exceed expenditure. The pattern for *N. violacea* is obscured by the dearth of precise probing rate data, and a lack of information indicating how frequently this species is able to forage at *M. hirtus* inflorescences.

Discussion

In terms of apparent nectar energy availability, nectarivores at Betty's Bay occupy a very patchy environment. *Erica perspicua* produces nectar that is more concentrated than that available in most plants pollinated by birds (Baker 1975; Hainsworth & Wolf 1979), yet standing crop volumes are generally small and variable. *Mimetus hirtus* has less concentrated nectar, with relatively large volumes available in most partially opened inflorescences early in the day, but much smaller volumes at other times and in most fully opened or closed inflorescences at any time (Collins 1983). *P. cafer* and *N. violacea* exploit this environment in different ways. For reasons suggested later, *N. violacea* appears to forage mainly in habitats where *E. perspicua* is dominant, while many *P. cafer* occupy feeding territories which incorporate stands of *M. hirtus*. Within these stands, there is a very pronounced preference for partially opened inflorescences (Collins 1983), with standing crop volumes being reduced significantly early in the day when probing by *P. cafer* is most frequent. Similar patterns of nectar depletion have been demonstrated for several other plant–nectarivore systems (e.g. Ford 1979; Collins & Briffa 1982, 1983b, 1983c). Mean standing crop volumes for *E. perspicua*, however, remain relatively constant throughout the day, suggesting that nectar production offsets depletion by *N. violacea*.

The technique used to estimate nectar energy intake by nectarivores at Betty's Bay assumed that all available nectar in each flower or inflorescence was ingested as a result of a single probe. This may not always have been the case, although the

results of spot checks on 10 partially opened *M. hirtus* inflorescences and 10 *E. perspicua* flowers, just visited by nectarivores at approximately 06h30 on 21 September, suggest that this is a reasonable assumption ($\bar{X} \pm \text{SD}$ standing crops: *M. hirtus* $0,8 \pm 0,9 \mu\text{l}$; *E. perspicua* $0,2 \pm 0,4 \mu\text{l}$; Collins, unpublished data). Some probes may also have been associated with foraging for arthropods rather than nectar, as appears to be the case with certain Australian honeyeaters (Collins & Briffa 1982), although few invertebrates were detected on *E. perspicua* flowers ($1,0 \pm 0,9$ thrips/flower) or *M. hirtus* inflorescences ($2,2 \pm 1,6$ bugs/inflorescence) during the study period (Collins, unpublished data). Despite these reservations, it appears likely that nectar intake by *P. cafer* is greatest early in the morning. This pattern resembles that exhibited by many other nectarivores in the laboratory and field (e.g. Collins & Clow 1978; Collins & Morellini 1979; Hainsworth & Wolf 1979; Collins, Cary & Packard 1980; Collins & Briffa 1983b). The shortage of probing rate data, and probable bias introduced by my inability to follow *N. violacea* for more than one or two minutes at a time, however, make it difficult to predict whether the pattern of nectar intake for this species is similar.

The practice of using time-budget data as a basis for estimating energy expenditure by free-ranging birds is now widely accepted (e.g. Wolf, Hainsworth & Gill 1975; Walsberg 1977; Hainsworth & Wolf 1979; Frost & Frost 1980; Ford 1981; Collins & Briffa 1983b). Nevertheless, Collins & Briffa (1983a) have indicated several possible deficiencies in the methodology employed in some instances. In particular, metabolic rate and time-budget data have often been gathered at different times of year. As seasonal variations in metabolic rate and insulation are known to occur, this has probably led to some serious errors in energy budget estimates (Weathers 1980; Collins & Briffa 1983a, 1983b), and may account for discrepancies between estimates based on time-budget data and those involving the use of doubly labelled water that have been reported (e.g. Weathers & Nagy 1980). Empirical unit perching and flight costs for *P. cafer* and *N. violacea* were not available for use in this study, so that predictive equations based on informa-

tion obtained for other species had to be employed. Estimated energy expenditures should therefore be treated with caution, even though predicted unit costs for *N. violacea* were similar to those obtained directly for the bronzy sunbird (*Nectarinia reichenowi*) (Wolf, Hainsworth & Gill 1975), and the similar-sized brown honeyeater (*Lichmera indistincta*) (Collins & Briffa 1983a), studied at similar times of year.

Predicted energy expenditures for territorial male and female *P. cafer*, and male *N. violacea*, clearly reflect variations in the amounts of time devoted to flight. Expenditures also appear to be minimized at times when nectar availability is least. Nevertheless, it would seem that energy storage which results from nectar intake probably occurs only during the early part of each day, after which birds incur energy deficits. This situation is reminiscent of that demonstrated previously for *Lichmera indistincta* (Collins & Briffa 1983b), and would help to explain why *P. cafer* and *N. violacea* caught after midday sometimes weigh slightly less than those trapped during the morning (Collins, unpublished observations). Should *P. cafer* be unable to satisfy its preference for partially opened *M. hirtus* inflorescences (Collins 1983), it would experience great difficulty in accumulating energy at any time of day, even if large numbers of fully opened *M. hirtus*-inflorescences or *E. perspicua* flowers were available. *P. cafer* was occasionally seen hawking for insects. It is possible that the insects contribute towards overall energy intake, and it would be interesting to ascertain whether the incidence of hawking increases during the afternoon.

Total diurnal energy requirements by nectarivores are influenced greatly by body size. The larger *P. cafer* studied at Betty's Bay in September assured themselves of adequate energy supplies by defending territories in areas containing relatively rich supplies of *M. hirtus* nectar, despite the additional expense associated with territoriality. There are sound energetic reasons why *P. cafer* should adopt this strategy, rather than randomly forage in both *M. hirtus* and *E. perspicua*. The foraging rate required for a given nectarivore to acquire adequate energy supplies increases exponentially as the available standing crop energy content decreases (Figure 4). Let us suppose that a male *P. cafer* weighing 41,8 g was obliged to rely entirely on nectar energy provided by *E. perspicua*. If 3,8 J of energy were available per flower, as at 06h30 on 19 September, the bird would have to forage at a mean rate of 0,81 probes/s throughout the day in order to acquire sufficient energy. This rate would be approximately four times that predicted for a 9,9 g male *N. violacea* under the same conditions. If allowance were to be made for the effect of extra flight probably required to visit additional flowers, the required rate would be even greater. In either case, the rate would be more than 11 times the observed overall mean value for the same male *P. cafer* foraging in partially opened *M. hirtus* inflorescences. In practice, the difference in foraging rate would be greater, as these calculations make no allowance for slight decreases in *E. perspicua* standing crop energy that occur during the day. It is most unlikely that *P. cafer* could maintain the foraging rates required to survive on a diet of *E. perspicua* nectar, and still find time for other activities.

In a similar fashion, it could be shown that *P. cafer* would be at a distinct disadvantage if obliged to rely entirely on nectar from fully opened *M. hirtus* inflorescences. By selectively probing partially opened inflorescences, this species appears to minimize foraging time and presumably maximize foraging efficiency (Schoener 1971; Hainsworth & Wolf 1979). It has been suggested elsewhere that appropriate inflorescences are

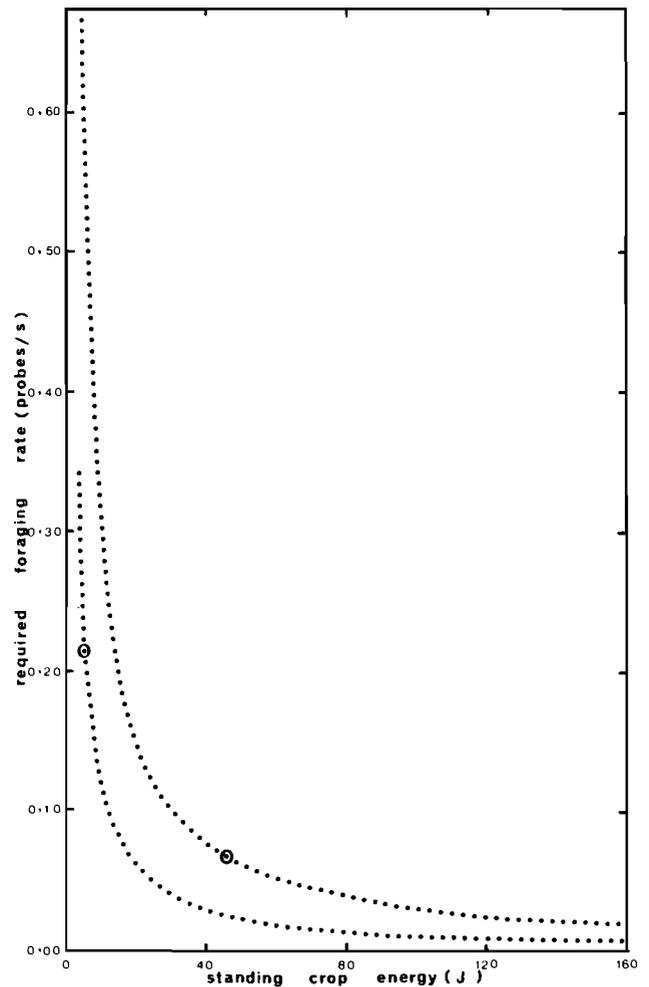


Figure 4 Relationships between required rates of floral probing and available standing crop nectar energy for male *P. cafer* (upper curve) and male *N. violacea* (lower curve). Curves have been constructed on the basis of data presented for 22–23 September in Table 2. Mean probing rates actually exhibited by birds in this study are denoted by \odot .

selected on the basis of their physical appearance (Collins 1983). Presumably, the consistently high nectar rewards in territories defended against competitors help to reinforce this behaviour (Hainsworth & Wolf 1979). It is possible that *P. cafer* may further increase its foraging efficiency by selective probing of partially opened inflorescences that have not been probed recently, although this hypothesis has yet to be tested.

Energetically, it would be of benefit to *N. violacea* if it could forage in *M. hirtus*, as the required foraging rate would be much lower than in *E. perspicua*. Nevertheless, resource partitioning appears to conform to a pattern described for several other plant–animal systems (e.g. Gill & Wolf 1975; Ford 1979), with the smaller, subordinate *N. violacea* frequently being chased from areas containing *M. hirtus* by territorial *P. cafer*. Although obliged to utilize the less energetically rewarding nectar of *E. perspicua* for much of the time, *N. violacea* could not survive if this were the only energy source (Figure 4 and Table 3). Members of this species possibly obtain sufficient energy during their infrequent visits to *M. hirtus*, the only other nectar source in the area, to make up the deficit. Nevertheless, there are other possible reasons for the apparent imbalance between energy intake and expenditure for *N. violacea*. For instance, *N. violacea* may ingest significant amounts of arthropods and fruits to supplement nectar energy intake. Estimated probing rates and time-budget data could also be inaccurate and lead to significant errors in energy-budget

estimates. Much further study will be required, however, before these possibilities can be accurately assessed.

This study has provided an indication of probable differences in energy requirements and resource utilization by *P. cafer* and *N. violacea*. Nevertheless, there is a clear need for precise estimates of unit perching and flight costs for both species, and their integration with time-budget data gathered over longer intervals and with additional birds.

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References

- ASCHOFF, J. & POHL, H. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29: 1541–1552.
- BAKER, H.G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7: 137–141.
- BURGER, A.E., SIEGFRIED, W.R. & FROST, P.G.H. 1976. Nest-site selection in the Cape sugarbird. *Zool. afr.* 11: 127–158.
- CHEKE, R.A. 1971. Temperature rhythms in African montane sunbirds. *Ibis* 113: 500–506.
- COLLINS, B.G. 1981. Nectar intake and water balance for two species of Australian honeyeater, *Lichmera indistincta* and *Acanthorhynchus superciliosus*. *Physiol. Zool.* 54: 1–13.
- COLLINS, B.G. 1983. Pollination of *Mimetes hirtus* (Proteaceae) by Cape sugarbirds and orange-breasted sunbirds. *Jl S. Afr. Bot.* 49: 125–142.
- COLLINS, B.G. & BRIFFA, P. 1982. Seasonal variations in abundance and foraging of three species of Australian honeyeaters. *Aust. Wildl. Res.* 9: 557–569.
- COLLINS, B.G. & BRIFFA, P. 1983a. Seasonal variations in the energetics of an Australian nectarivorous bird, *Lichmera indistincta*. *Comp. Biochem. Physiol.* 74A: 731–738.
- COLLINS, B.G. & BRIFFA, P. 1983b. Seasonal and diurnal variations in the energetics and foraging activities of the brown honeyeater, *Lichmera indistincta*. *Aust. J. Ecol.* 8: 103–111.
- COLLINS, B.G. & BRIFFA, P. 1983c. Nectar utilization and pollination by Australian honeyeaters and insects visiting *Calothamnus quadrifidus* (Myrtaceae). *Aust. Wildl. Res.* (in press).
- COLLINS, B.G., CARY, G. & PACKARD, G. 1980. Energy assimilation, expenditure and storage by the brown honeyeater, *Lichmera indistincta*. *J. Comp. Physiol.* 137: 157–163.
- COLLINS, B.G., CARY, G. & PAYNE, S. 1981. Metabolism, thermoregulation and evaporative water loss in two species of Australian nectar-feeding birds (family Meliphagidae). *Comp. Biochem. Physiol.* 67A: 629–635.
- COLLINS, B.G. & CLOW, H. 1978. Feeding behaviour and energetics of the western spinebill, *Acanthorhynchus superciliosus*. *Aust. J. Zool.* 26: 269–277.
- COLLINS, B.G. & MORELLINI, P. 1979. The influence of nectar concentration and time of day upon energy intake and expenditure by the singing honeyeater, *Meliphaga virescens*. *Physiol. Zool.* 52: 165–175.
- FORD, H.A. 1979. Interspecific competition in Australian honeyeaters — depletion of common resources. *Aust. J. Ecol.* 4: 145–164.
- FORD, H.A. 1981. Territorial behaviour in an Australian nectar-feeding bird. *Aust. J. Ecol.* 6: 131–134.
- FROST, S.K. & FROST, P.G.H. 1980. Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae). *Oecologia* 45: 109–116.
- GILL, F.B. & WOLF, L.L. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56: 333–345.
- HAINSWORTH, F.R., COLLINS, B.G. & WOLF, L.L. 1977. The function of torpor in hummingbirds. *Physiol. Zool.* 50: 215–222.
- HAINSWORTH, F.R. & WOLF, L.L. 1979. Feeding: an ecological approach. *Advances in the Study of Behaviour* 9: 53–96.
- HART, J.S. & BERGER, M. 1982. Energetics, water economy and temperature regulation during flight. In: *Proc. XVIIth Int. Ornithol. Congr.* ed. Voous, K.H., pp.189–199, E.J. Brill, Leiden.
- KLEIBER, M. 1961. *The Fire of Life: An Introduction to Animal Energetics*. Wiley, New York.
- MOSTERT, D.P., SIEGFRIED, W.R. & LOUW, G.N. 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape sugarbird. *S. Afr. J. Sci.* 76: 409–412.
- SCHMIDT-NIELSEN, K. 1979. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, London.
- SCHOENER, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369–404.
- WALSBERG, G.E. 1977. Ecology and energetics of contrasting social systems in *Phaenopepla nitens* (Aves: Ptilonotidae). *Univ. California Publ. Zool.* 108: 1–63.
- WEAST, R.C. 1975. *Handbook of Chemistry and Physics*. CRC, Cleveland.
- WEATHERS, W.W. 1980. Seasonal and geographical variation in avian standard metabolic rate. In: *Proc. XVIIth Int. Ornithol. Congr.*, ed. Nohring, R., pp.283–286, Springer Verlag, Berlin.
- WEATHERS, W.W. & NAGY, K.A. 1980. Simultaneous doubly labelled water and time-budget estimates of daily energy expenditure in *Phaenopepla nitens*. *Auk* 97: 861–867.
- WIENS, D., ROURKE, J.P., CASPER, B.B., RICKART, E.A., LA PINE, T.R. & PETERSEN, T.J. 1982. Non-flying mammal pollination of southern African proteas: a non-coevolved system. *An. Miss. Bot. Gard.* (in press).
- WOLF, L.L. 1975. Energy intake and expenditures in a nectar-feeding sunbird. *Ecology* 56: 92–104.
- WOLF, L.L. & HAINSWORTH, F.R. 1971. Time and energy budgets of territorial hummingbirds. *Ecology* 52: 980–988.
- WOLF, L.L., HAINSWORTH, F.R. & GILL, F.B. 1975. Foraging efficiencies and time budgets in nectar-feeding birds. *Ecology* 56: 117–128.