Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications

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Foraging success is the first indicator of food availability which in turn is a major determinant of clutch size, timing and output of reproduction as well as habitat selection, density and survival. Yet it has been rarely investigated among insectivorous birds and never along a latitudinal gradient. To allow a meaningful comparison between a tropical and a temperate guild of small foliage gleaners, the data were recorded in similar conditions and restricted to adult birds actively foraging, in the understory of primary rain forest (French Guiana) and old stands of broad leaved forest (France) during the breeding season.
The mean attack rate of tropical species is 4 to 6 times lower than that of their temperate equivalents. The differences are highly significant, consistent over every species, and cannot be attributed to the birds' body size or prey size. The temperate species are more specialized on caterpillars and their foraging success has a lower variance than that of tropical species, suggesting that food resources may be on average higher, richer and more evenly distributed in temperate forests. Foraging speed is significantly higher in temperate than in tropical species and is correlated with attack rate and body size only among the latter. There are no consistent relationships between attack rate and foraging height, capture techniques or substrates used. Tropical species make a greater use of dead leaves and epiphytes than do temperate ones, as well as of the most expensive capture modes (probing, striking, sallying). They also take more prey under the leaf surface and have a larger foraging niche breadth than their temperate counterparts.
Contrary to the widely assumed superabundance and stability of food resources in the tropics, it is suggested that a reduced prey availability (density, detectability, distribution, seasonality) may be a major cause of the lower foraging success of rain forest birds. Accordingly this constraint is likely to limit their reproductive rate and would in part explain their very low clutch size.

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Introduction

Foraging success is one of the basic components of individual fitness and adaptation to the environment. It is among the proximate factors governing important aspects of population ecology such as habitat selection, density, breeding success and survival rate. It gives an index of prey availability and this food supply is widely considered as the main determinant of clutch size, reproductive success and timing of the breeding season

(Lack 1968, Klomp 1970, Murphy and Haukioja 1986, Blondel et al. 1987).

Yet in the many studies on the foraging niche or evolutionary ecology of small insectivorous birds, hunting speed and success rate are seldom measured and only investigated among other variables entered in multivariate analyses of foraging behaviour (but see Morse 1968, Eckhardt 1979, Robinson and Holmes 1982). The

Tab. 1. Species studied. Size: means ± SD of the three main morphological measurements from birds caught in mist nets (number in brackets) for the Guianan sample and ranges (Géroudet 1974) for the French set (only median masses were subsequently used). Observations: cumulative number and duration of individual foraging sequences followed (see text).

(a) GUIANA		Size			Observations	
		Mass (g)	Wing (mm)	Bill (mm)	Number of periods	Total time (s)
Philydor erythrocercus (12) Rufous-rumped foliage gleaner		26.4±4.6	84.9±2.8	18.3±2.3	24	1872
Philydor ruficaudatus (4) Rufous-tailed foliage gleaner		24.4±3.0	90.7±7.0	15.6±1.4	20	1825
Automolus infuscatus (16) Olive-backed foliage gleaner		31.6±2.8	89.8±2.3	19.4±1.3	18	1562
Cymbilaimus lineatus (5) Fasciated antshrike		35.0±2.8	73.5±1.2	25.6±2.0	15	1564
Thamnophilus murinus (13) Mouse-colored antshrike		19.3±1.7	63.8±3.0	18.0±0.5	14	2334
Thamnomanes ardesiacus (22) Dusky-throated antshrike		17.7±1.5	74.6±1.7	16.3±0.7	21	2186
Thamnomanes caesius (18) Cinereous antshrike		16.2±1.9	73.2±3.1	15.3±1.2	49	5035
Myrmotherula guttata (10) Rufous-bellied antwren		11.0±1.3	52.5±1.8	13.8±0.8	20	2432
Myrmotherula gutturalis (16) Brown-bellied antwren		9.2±1.0	54.8±1.5	12.4±0.9	25	2262
Myrmotherula axillaris (9) White-flanked antwren		7.8±0.7	53.4±3.5	13.3±1.0	21	1560
Myrmotherula longipennis (33) Long-winged antwren		9.4±1.1	60.5±2.0	12.6±0.7	47	3425
Myrmotherula menetriesii (13) Grey antwren		8.6±0.5	55.4±1.9	13.5±0.8	50	4300
Hypocnemis cantator (10) Warbling antbird		11.6±0.7	55.1±1.8	14.1±0.7	29	2920
Hylophylax naevia (16) Spot-backed antbird		13.1±1.0	60.8±1.3	14.8±0.7	24	1701
Hylophylax poecilonota (24) Scale-backed antbird		16.7±1.1	66.2±1.7	16.7±0.9	20	3330

(b) FRANCE	Size			Observations	
	Mass (g)	Wing (mm)	Bill (mm)	Number of periods	Total time (s)
Aegithalos caudatus Long-tailed tit	6–10	55–67	6– 8	26	3601
Parus caeruleus Blue tit	9–16	60–73	8– 9	75	6405
Parus major Great tit	15–22	70–82	10–11	74	6390
Parus palustris Marsh tit	9–13	56–68	9–10	30	2448
Sylvia borin Garden warbler	16–25	72–83	12–14	16	1420
Sylvia atricapilla Blackcap	15–25	69–80	12–14	18	1442
Phylloscopus collybita Chiffchaff	6– 9	52–67	10–12	55	6832
Phylloscopus trochilus Willow warbler	7–11	62–72	10–12	30	3490
Phylloscopus sibilatrix Wood warbler	8–12	71–79	11–13	37	3091
Fringilla coelebs Chaffinch	17–30	75–94	12–14	48	5233

main reason for this lack of interest probably comes from its expected variability with almost every life history parameter as well as environmental biotic or abiotic factor. Thus it has been shown to vary according to the species (size, morphology), sex, diet, habitat, substrate, foraging mode, prey characteristics (size, conspicuousness, activity, velocity, density and accessibility), time of day, ambient temperature, weather conditions or season (Morse 1968, Alatalo 1982, Graber and Graber 1983, Greenberg and Gradwohl 1983, Avery and Krebs 1984, Holmes 1986). This hunting success, or at least searching intensity, is also higher when the birds are feeding young (Root 1967, Robinson 1986), during the premigratory fattening period (Bairlein 1985), on continents than on small islands (Morse 1981) or when feeding in flocks vs solitarily (Herrera 1979).

However to the best of my knowledge, it has never been suggested that the overall foraging rate of rain forest insectivores might be significantly lower than that of their temperate forest counterparts. With so many interdependent factors potentially influencing this foraging success, the hypothesis may seem hopelessly untestable. Yet, if it were shown to be true, such a lower foraging rate would raise questions of fundamental interest such as: Is prey availability for insectivorous birds during the breeding season really lower and more limiting in tropical than in temperate forests? Is the very low clutch size of tropical forest birds related to this low food availability? Is the latitudinal decrease of clutch size in birds partly related to a decrease in food supply?

Indeed, prey accessibility, daily time available for feeding and temperature dependent energy requirements are among the factors closely related to the food supply that must also be involved in the explanation of the latitudinal gradient in clutch size (Møller 1984). Most of the variability of individual foraging rates is related to foraging intensity, e.g. how much a bird inserts short periods of rest, vigilance, social interactions, singing, etc. ... within or between foraging bouts. However, according to optimal foraging theory, when an animal is really and actively hunting, it is assumed to forage as efficiently as possible. Hence provided one can identify and separate non foraging behaviours from actual foraging sequences, and if other main sources of bias are removed (age, habitat, diet, hunting mode) or controlled (prey size), success rates are expected to become comparable between species.

Materials and methods

Study areas and habitats

To obtain a representative sample and to reduce any possible bias, observations were made within at least 30 separate plots, spread over a forest area of more than 100 km² in each country and during three different years. Three localities were investigated in northern

(piste de Saint-Elie, southwest of Sinnamary), north eastern (Arataye River, 100 km south of Cayenne) and south central (Saül) French Guiana. Temperate species were studied in a heavily forested area of France (Regional Park of the Forêt d'Orient, northeast of Troyes).

In both countries, only birds of the understory, within large tracts of continuous, natural, lowland, broad-leaved forests away from edges, have been recorded. Only the oldest stands of high, mature, humid forest were selected. In Guiana, they included various types of rich undisturbed primary rain forest, 35 to 50 m high, harboring several hundred species of trees and numerous tree fall gaps. In France, the managed forest was 20–30 m high and dominated by oaks (*Quercus pedunculata*) and hornbeams (*Carpinus betulus*) with locally many aspens (*Populus tremula*), birches (*Betula alba*) and alders (*Alnus glutinosa*).

Species and timing

The study was designed to compare small foliage gleaners which are usually the most abundant insectivorous birds in both temperate and tropical forests. The guild was restricted to: 1) passerines of less than 40 g mass; 2) locally common taxa; 3) individuals foraging between 1 and 20 m high; 4) insectivores that obtain most if not all of their prey from leaf surface, epiphytes or limbs; 5) active searchers (sensu Eckhardt 1979); 6) birds whose original habitat was mature forest (understory or small natural gap). Those species were excluded which were 1) partly frugivorous or granivorous during the breeding season; 2) largely feeding on bark, litter, flying insects or following army ants, i.e. mostly trunk-foragers, ground dwellers and flycatchers; 3) usually foraging in the high canopy and thus difficult to follow; 4) too rare or inconspicuous to provide enough data (minimum of 10 sample periods).

The birds studied belong to the families Furnariidae and Formicariidae in Guiana (15 species), and Paridae, Sylviidae and Fringillidae in France (10 species, Tab. 1). They represent the main (i.e. by far the most numerous) species of both the French and the Guianan guilds as strictly defined above (Thiollay 1988 and unpubl. data). In both forests, the species sampled do not differ significantly in habitats, diets or behaviours from other minor members of the guild. They cover nearly all the existing adaptations within the limited ecological characteristics chosen.

The data were gathered only during the main nestling and early fledging phases of the breeding cycles (personal breeding records for all the species). This study period extended in France from mid-May (after all trees had developed their foliage) to mid-July (fledging of the second broods) 1984 to 1987, i.e. late spring to early summer, and, in Guiana, from September to December 1983 to 1986 (late dry-early rainy season). Insect abundance peaks sharply in late spring in temperate forests and in early rains in neotropical rain forests (Smythe in

Leigh et al. 1983). The foraging success of birds was thus studied at a season of maximum food availability but also of maximum food requirement. The observations extended over three years to take into account the interannual variability of food supply and to avoid any atypical conditions. No noteworthy high level of insect abundance and no outbreak of defoliators were noticed either in France or Guiana, during the study. Observations were made at any hour between sunrise and sunset, provided the weather was clear and the birds were active.

Recording and parameters

Focal individuals (Altmann 1974) were located at random, then followed with 10×40 binoculars as long as they could be kept in full sight (behaviour clearly identifiable), were not resting, preening, singing, alarming or exploiting local prey concentrations and were not disturbed by my presence. Movements and prey attacks were recorded on a continuously running tape, then timed to the nearest second and counted. Only adults were observed (presumed to have a higher hunting success than younger birds), actively searching for food either for themselves or to feed young. Only sequences of at least 60s of active foraging by the same individual, followed without a break and after excluding bouts of handling time, were kept for analysis. Any stop that could be interpreted as rest, social interaction, vigilance or territory surveillance, was also discarded from the sample period. Under these restrictive conditions, such long foraging sequences have proved to be difficult to obtain (and many shorter observations were not used). Thus 472 h spent searching in the forest of Guiana provided an overall 397 sequences totalling 639 min, whereas 673 min in 409 periods were obtained in France during a 413 h search (Tab. 1).

To ensure the independence of all the observations, each bird was recorded only once in a given patch, no more than one individual of any species was followed in a plot and no area was searched more often than once a week. The following data were recorded for each foraging bout: species, sex, date, hour, locality, frequency of calls, presence of accompanying birds (mate, family, flock, ...), type of forest, habitat structure (minimum and maximum canopy heights, density of the three main strata), height of the foraging bird (extremes during the observation period, visually estimated), duration of the actual foraging period, hunting method, number and length of searching moves, number of attacks, mode and substrate of prey capture attempts, size and type of prey items. Three classes of tree (1–5, 5–20 and > 20 cm dbh) and branch sizes ($\leq$ 1, 2–5 and > 5 cm in diameter) were distinguished, as well as upper and lower part of trunks or inner, middle and outerparts of branches. The speed of the search was given by the rate of moves divided in three categories: hops = jumping along or between branches (< 1 meter long), short flights (1 to 5 m), usually within a same patch of vegetation (tree or group of trees) and long flights (> 5 m), often at the end of a sequence because the bird was then lost. Total distances moved by birds could not be accurately estimated. Movements directed toward prey (attacks), or made by a bird looking around but not shifting along the branch, were not considered as moves.

Attacks included both successful captures (the greater part) and some unsuccessful attempts because it was not always possible to know if small arthropods were actually taken. Thus our capture rate is to be considered as a rate of prey attack or encounter. A few foraging motions which were uncertain capture attempts were recorded as moves. Consequently, most capture rates are conservative, but this source of bias is likely to be similar between the two sets of species under comparison.

Prey capture manoeuvres are divided into:
Glean = a standing or moving bird picking a stationary prey item from a substrate;
Probe = the bird manipulates the substrate, pecking or rummaging in dead wood, bark, epiphytes and dead leaves as well as tearing off or uncurling leaves rolled or glued by larvae;
Snatch = the bird hops, flits or hangs to reach the prey on the substrate. It is probably more energetically expensive than a glean but does not involve a true flight;
Hover = prey capture from a substrate while in stationary flight (= hoverglean);
Strike = short flight to pick up a prey from a substrate on which the bird does not perch (= sally glean);
Chase = pursuing a prey flushed by the bird, usually in a long downward flight;
Sally = attack of a flying insect around the foliage (= hawking, but at a shorter distance than most of the flycatchers do).

The substrates were classified into: upper or lower side of green, dead and curled leaves, bark (of branches or trunks), twigs (including tips of branches, petioles of leaves and bugs), vines (all sizes), epiphytes (including mosses and lichens), litter and air. Arthropods were identified as precisely as possible. Prey sizes were ranked into four body length classes estimated from the bird's bill length: 1 = 1 to 10 mm (includes small prey, quickly swallowed and unseen); 2 = 11–20 mm; 3 = 21–30 mm; 4 > 30 mm. Length is a poor predictor of mass in such a diverse assemblage and the caloric value would have been the most significant parameter (5.0 to 6.3 kcal g^{-1} ash free dry mass, Calver and Wooller 1982, Graber and Graber 1983). However I calculated a rough coefficient relating size to biomass after weighing a sample of 50 arthropods of each category, randomly caught in sweep nets from the foliage in each of the two study areas, then pooling the samples (not significantly different from each other). The multiplying factor thus drawn for length classes 1 to 4 was respectively 1, 4, 12 and 20. It gives a better estimate of relative prey sizes

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Tab. 2a. Mean capture rates per minute of temperate foliage gleaners. The rates are first calculated on individual sample sequences (± SD), then on the sum of all sample periods and on this last value corrected for bird and prey sizes i.e. overall rate

$$\times \ \frac{\text{mean prey size*}}{\sqrt[3]{\text{species' body weight**}}}$$

* (see last column and text)   ** (see Tab. 1)

FRANCE	Capture rate from:			Mean prey size
	Individual samples (± SD)	Overall sample time	Corrected value	
Aegithalos caudatus	2.61 (±1.42)	2.53	1.94	1.53
Parus caeruleus	2.55 (±0.92)	2.52	3.91	3.65
P. major	2.29 (±0.90)	2.22	4.08	4.91
P. palustris	2.07 (±0.84)	2.03	3.16	3.46
Sylvia borin	2.24 (±1.23)	2.28	2.39	2.89
S. atricapilla	3.10 (±1.69)	2.95	2.99	2.75
Phylloscopus collybita	3.71 (±1.75)	3.29	2.68	1.63
P. trochilus	2.70 (±0.83)	4.03	6.30	3.25
P. sibilatrix	2.16 (±0.86)	2.14	3.14	3.15
Fringilla coelebs	2.25 (±0.89)	2.18	2.25	2.97
All species mean (± 99% confidence limit)	2.57 (±0.42)	2.62 (±0.51)	3.28 (±1.03)	3.02 (±0.79)
Difference between temperate and tropical species t, 2 tailed df = 21	14.14	12.10	10.63	1.93
P	< 0.001	< 0.001	< 0.001	> 0.05

Tab. 2b. Capture rates of tropical insectivores (see Tab. 2a). *Heaviest species excluded from the calculation of the means (see text).

GUIANA	Capture rate from:			Mean prey size
	Individual samples (± SD)	Overall sample time	Corrected value	
Philydor erythrocercus	0.55 (±0.53)	0.61	0.33	1.63
P. ruficaudatus	0.54 (±0.41)	0.56	0.79	4.12
*Automolus infuscatus**	0.30 (±0.37)	0.31	0.54	5.50
*Cymbilaimus lineatus**	0.22 (±0.36)	0.23	0.51	7.25
Thamnophilus murinus	0.31 (±0.28)	0.28	0.65	6.27
Thamnomanes ardesiacus	0.62 (±0.73)	0.41	0.39	2.47
T. caesius	0.42 (±0.45)	0.39	0.22	1.46
Myrmotherula guttata	0.37 (±0.48)	0.44	0.26	1.33
M. gutturalis	0.43 (±0.47)	0.48	0.30	1.33
M. axillaris	0.96 (±0.63)	0.99	0.77	1.54
M. longipennis	0.81 (±0.55)	0.77	0.67	1.84
M. menetriesii	0.91 (±0.64)	0.92	0.81	1.80
Hypocnemis cantator	0.71 (±0.66)	0.88	0.63	1.63
Hylophylax naevia	0.50 (±0.36)	0.44	0.24	1.30
H. poecilonota	0.37 (±0.29)	0.29	0.51	4.50
13 species mean (± 99% confidence limit)	0.58 (±0.15)	0.57 (±0.17)	0.51 (±0.16)	2.40 (±1.12)

and, being similar between the two sets of species, it is adequate for our purpose.

For statistical analyses, all parametric tests were taken from Sokal and Rohlf (1969). When assumptions of normal distribution were not met, the rates were square root transformed or non parametric tests were used (Siegel 1956).

Results

Hunting success and prey size

The mean capture rates of the temperate insectivores studied were significantly higher than those of all the rain forest species with no overlap between the two sets (Tab. 2). The mean for all tropical species was 4.4 to 4.6

Capture rate

Temperate: $R^2 = 0.17$
$y = 4.42 - 0.76x$

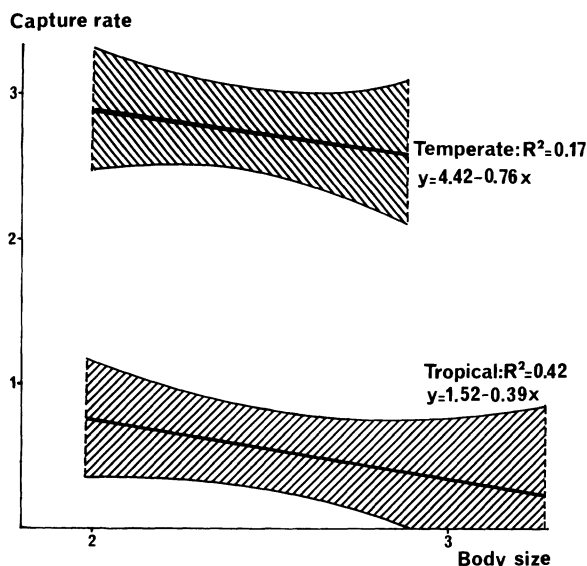Tropical: $R^2 = 0.42$
$y = 1.52 - 0.39x$

Body size

Fig. 1. Mean overall capture rate per minute as a function of the cube root of body size and 95% confidence zones for the regression lines, in the temperate and tropical set of insectivores.

times lower than that of the temperate species. This difference of 343–360% is even larger when the raw rates are weighted for body size, or prey size or an index of both (Tab. 2) to minimize any dissimilarity in diet and morphology between temperate and tropical species.

The two biggest tropical species (*Automolus* and *Cymbilaimus*) whose masses are greater than the maximum mass of the temperate species considered, have been excluded from the computation of the mean capture rates, body and prey sizes to increase the morphological similarity of the two groups. Likewise, the capture rates of individual sequences being quite variable, I used in subsequent correlations the mean rates calculated over all the sample periods pooled for a given species. They probably give the most conservative estimate of a species' overall capture rate.

If the two groups are so different, what is the level of similarity between the species within each group? The variances of the capture rates are not homogeneous (F = 4.44 and 6.83 for temperate and tropical species respectively, P > 0.05). Therefore I performed a Kruskal-Wallis one way ANOVA on the 409 observations from the 10 temperate species and 364 observations from the 13 smallest tropical species. The null hypothesis that within each group, at the 95% level of significance, all the species come from the same population cannot be rejected (temperate: H = 14.91, df = 9; tropical: H = 18.14, df = 12). Thus the two groups of species may be considered as sufficiently homogeneous and their average hunting successes is well distinct from each other.

The mean capture rates tend to be inversely corre-

lated with *body size* (Fig. 1), but the Spearman rank correlation coefficient is significant only for tropical species ($r_s = -0.68$, P < 0.01, 1 tailed) and not for temperate ones ($r_s = -0.39$, P > 0.05). However, the mean body mass of the 10 temperate species (14.3 ± 6.1 g) is not significantly different (t = 0.17, df = 21, P > 0.85) from the mean mass of the subset of 13 tropical species used here (14.7 ± 6.0 g), and no species of one group falls outside the size range of the other. Thus differences in body size cannot be involved in the markedly different capture rates of tropical and temperate species.

The mean *prey size* of each species is given here by $(1n_1 + 4n_2 + 12n_3 + 20n_4) / (n_1 + n_2 + n_3 + n_4)$ where n are the numbers of prey of size 1 to 4 and 1 to 20 are the average coefficients deriving masses from lengths (see Methods). Capture rates tend to be inversely correlated with mean prey size, but more weakly than with body

Prey size

Temperate

$y = 0.08 + 1.23x$
$R^2 = 0.19$
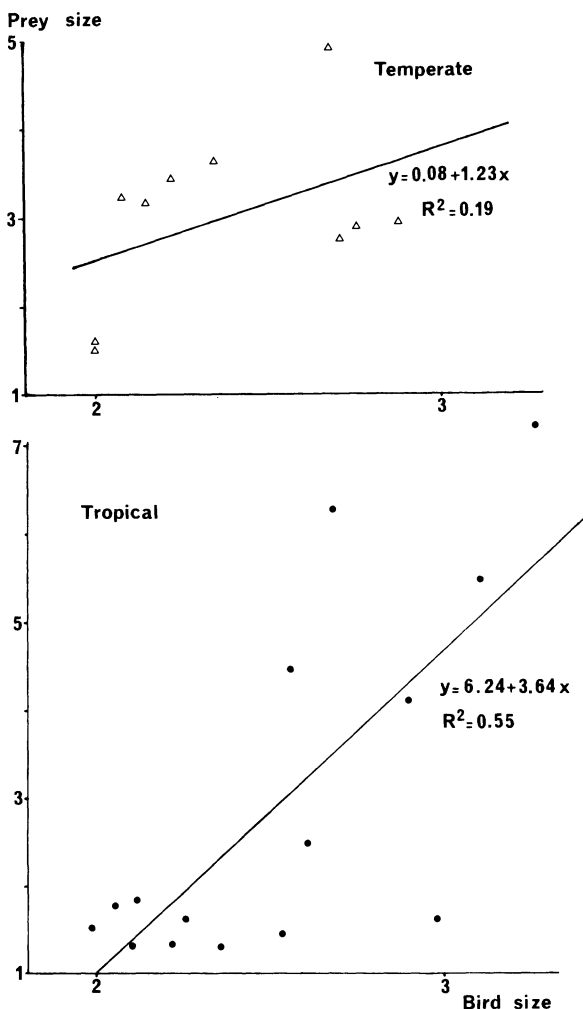
Tropical

$y = 6.24 + 3.64x$
$R^2 = 0.55$

Bird size

Fig. 2. Linear regression between the mean index of prey size and the bird size expressed as the cube root of body size, for the 10 temperate and 15 tropical species.

Tab. 3. Diets of the temperate and tropical species, from field identification of large prey taken by birds under observation.

Prey category	Tropical	Temperate
Caterpillars	33 (25.6%)	137 (73.3%)
Other larvae	10 (7.8%)	28 (15.0%)
Grasshoppers, mantids	34 (26.4%)	
Cockroaches, cicadas	11 (8.5%)	
Small butterflies	10 (7.8%)	3 (1.6%)
Other insects	19 (14.7%)	17 (9.1%)
Spiders, Myriapoda	12 (9.3%)	2 (1.1%)

size and again significantly for tropical ($r_s = -0.49$, P < 0.05, 1 tailed) but not for temperate species ($r_s = -0.42$, P > 0.05). Moreover, the overall mean prey size (Tab. 2) is not significantly different between the temperate and the tropical groups (t = 1.41, df = 21, P = 0.15). So the lower capture rates of the latter is not a consequence of a larger prey size.

There is a positive correlation between the birds' body mass and their prey size (Fig. 2) but it is only significant for tropical species ($r_s = 0.66$, P < 0.01, 1 tailed) and not within the temperate group ($r_s = 0.26$). The same relationship holds between prey size and bill length (tropical species: $r_s = 0.68$; temperate species: $r_s = 0.04$).

The *diets* of the two groups have been assessed only through visual identification of prey captured by the individuals recorded during the study. The composition is strongly biased towards the largest items because the small insects were unlikely to be recognized. However, the mean prey size being similar between the two groups, we may expect to look at the same part of their diet. All the species have been pooled within each group because they all showed the same tendencies (Tab. 3).

The prey items of the tropical insectivores are more diversified than those of the temperate species (Shannon's index H' = 1.811 vs 0.846) and their distribution is strikingly different ($\chi^2_1 = 119.01$, P < 0.001 when grouped into 4 categories to avoid low frequencies). Caterpillars (mostly Geometridae) are much more prominent in the diet of all the temperate foliage gleaners. Their common use of this superabundant food source, often on the same trees (mainly oaks), may explain the lack of a significant correlation between their body mass or bill length and their average prey size. Conversely, the foliage of the rain forest seems richer in Orthoptera and Dictyoptera, among other large items, with a much lower biomass of caterpillars.

Besides prey abundance and its associated mean capture rates, the prey spatial distribution, reflected in the variance of hunting success is important to foraging birds which may be risk sensitive. The coefficients of variation of capture rates are on average more than two times higher in tropical ($\bar{X} = 97.4 \pm 27.9\%$) than in temperate species ($\bar{X} = 43.7 \pm 8.5$) and not overlapping (ranges: 65.6 to 163.6 vs 30.7 to 54.9, respectively). This

suggests that foraging tropical insectivores not only find suitable prey (or succeed in catching them) less frequently than similar species in the temperate guild, but that they also find them more irregularly.

Velocity and foraging behaviour

Foraging speed, or velocity (Eckhardt 1979, Morse 1968, 1981) is defined as the number of moves per minute (i.e. perch changes = hops + short flights). The few long flights, not always directly related to foraging, were not taken into account. This overall index is significantly higher in temperate (21.6 ± 2.4) than in the 13 smaller tropical species (11.1 ± 6.0; Mann Whitney U test, U = 5, P < 0.002). The variances of the foraging speeds are significantly homogeneous within the former group (F test, F = 2.13, P = 0.05) but not among the latter (F = 32.04, NS).

There is an overall positive correlation between foraging velocity and prey capture rate (Fig. 3), but within groups this correlation is only significant for tropical ($r_s = 0.88$, P < 0.01) and not for temperate species ($r_s = -0.16$, P > 0.05). One would expect that the larger the species, the slower its moving rate. Again this inverse correlation between speed and body size (untransformed masses) holds for tropical species ($r_s = -0.46$, P < 0.05, 1 tailed, including the 2 largest taxa) but not for the temperate set ($r_s = 0.10$, NS).

A multiple regression analysis was performed on the 25 species pooled together with capture rate as the dependent variable and body mass (W), prey size (P) and foraging speed (S) as the independent variables. Thus $R^2 = 0.58$ and the regression equation is: t = 0.77 − 0.57W + 0.09P + 0.11S. However, body mass is
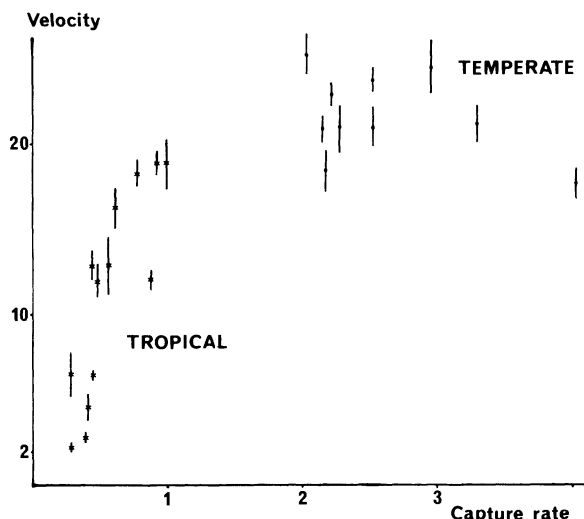

Fig. 3. Mean foraging velocity (hops + short flights min^{-1}) of 13 tropical (asterisks) and 10 temperate species (solid dots) plotted against their mean capture rate. Vertical bars = ± SE.

Tab. 4. Foraging speed of tropical and temperate species. Mean number of moves (hops + short flights) per minute, and proportion between hops and flights.

TROPICAL	Mean (± SD) hops + flights	Ratio hops/ flights	TEMPERATE	Mean (± SD) hops + flights	Ratio hops/ flights
Philydor erythrocercus	16.24 (±5.59)	11.21	*Aegithalos caudatus*	21.01 (±6.00)	9.93
P. ruficaudatus	12.92 (±6.91)	12.19	*Parus caeruleus*	23.65 (±5.75)	8.39
Automolus infuscatus	11.32 (±5.53)	10.91	*P. major*	22.93 (±6.47)	7.66
Cymbilaimus lineatus	8.15 (±3.09)	15.56	*P. palustris*	25.15 (±6.47)	5.19
Thamnophilus murinus	6.54 (±4.26)	6.71	*Sylvia borin*	20.89 (±5.38)	9.11
Thamnomanes ardesiacus	4.61 (±3.56)	1.88	*S. atricapilla*	24.46 (±6.69)	7.76
T. caesius	2.84 (±1.45)	0.73	*Phylloscopus collybita*	21.10 (±7.85)	11.78
Myrmotherula guttata	12.92 (±3.37)	8.18	*P. trochilus*	17.59 (±5.53)	8.93
M. gutturalis	11.97 (±5.17)	6.85	*P. sibilatrix*	20.79 (±5.52)	4.76
M. axillaris	18.82 (±6.85)	10.05	*Fringilla coelebs*	18.48 (±7.76)	7.31
M. longipennis	18.33 (±4.85)	10.16			
M. menetriesii	18.90 (±5.48)	11.92			
Hypocnemis cantator	12.02 (±3.46)	8.52			
Hylophylax naevia	6.56 (±1.21)	2.32			
H. poecilonota	2.25 (±1.27)	0.90			

correlated with the two other variables and performing the same analysis with only prey size and speed barely reduced the proportion of the capture rates' variation explained ($R^2 = 0.57$). A similar regression within each of the two groups recalls the correlations found for the tropical species ($R^2 = 0.74$) and lack of them for the temperate set ($R^2 = 0.21$).

Movement pattern. The ratio of hops to flights provides an additional parameter giving a more accurate picture of how the species moves while searching for prey (Tab. 4). It is also roughly proportional to the energy cost of foraging since a flight is more costly than a hop. If we assume that the average lenght of a short flight is about 5 times that of a hop (see Methods), this ratio would give an estimate of the distance travelled or the volume of foliage searched per unit time.

The mean ratio hop/flight is similar ($t = 0.11$, df = 23, $P > 0.90$) between tropical and temperate species (7.87 ± 4.58 vs 8.08 ± 2.09, Tab. 4) but the range is wider among the former (0.7–15.6) than the latter (4.8–11.8). There is a rather weak positive correlation between foraging speed and hop/flight ratio, over all the 25 species pooled ($r = 0.41$, $P < 0.05$, 2 tailed). This means that the level of foraging activity is indicated more by the frequency of hops than flights.

Following the classification of Eckhardt (1979) and Robinson and Holmes (1982), our species can be divided into four groups according to their foraging speeds:

1) Passive searchers which spend comparatively long times on each perch, quietly looking around, then flying to another perch. They perform on average less than 5 moves per minute and flights are about as frequent as hops (hop/flight ratio < 2); 3 tropical species are in this category (2 *Thamnomanes* and *Hylophylax poecilonota*).

2) Active searchers which move more or less continuously with usually more hops than flights (ratio between 5 and 12):

2a) 8 tropical species can be called slow searchers (6–13 moves min^{-1});
2b) 4 other tropical and 2 temperate species are intermediate searchers (16–19 moves min^{-1});
2c) the last 8 temperate species are rapid searchers (20–25 moves min^{-1}).

The mean capture rates of these four classes are respectively 0.36, 0.45, 1.58 and 2.50 captures min^{-1}, and the differences between them are highly significant (ANOVA with square root transformed data, $F (3,21) = 20.75$, $P < 0.001$). This recalls the positive correlation between foraging speed and capture rate and the segregation between the slower tropical species and their faster moving temperate counterparts.

The only slow or passive searchers in the French forests are flycatchers (*Muscicapa, Ficedula*), cuckoo (*Cuculus*) and oriole (*Oriolus*), all of them migrants of tropical origin. They are much better represented in the Old World rain forests and not included in our guild because of their hunting behaviour or large size.

The two *Thamnomanes* are noisy multispecies flock leaders, highly sensitive to disturbance. As against the antipredator protection they provide to other flock members and the time lost scanning around, they chase insects flushed by their flock mates (> 30% of captures), a behaviour which sometimes becomes kleptoparasitism. It is not true foliage gleaning but as they mostly catch prey on the vegetation, their low capture rate points to how their prey are usually rare or difficult to detect unless flushed.

Flocking. It was not possible to test for intraspecific differences of foraging behaviour or success rate be-

% occurrence

TROPICAL

TEMPERATE
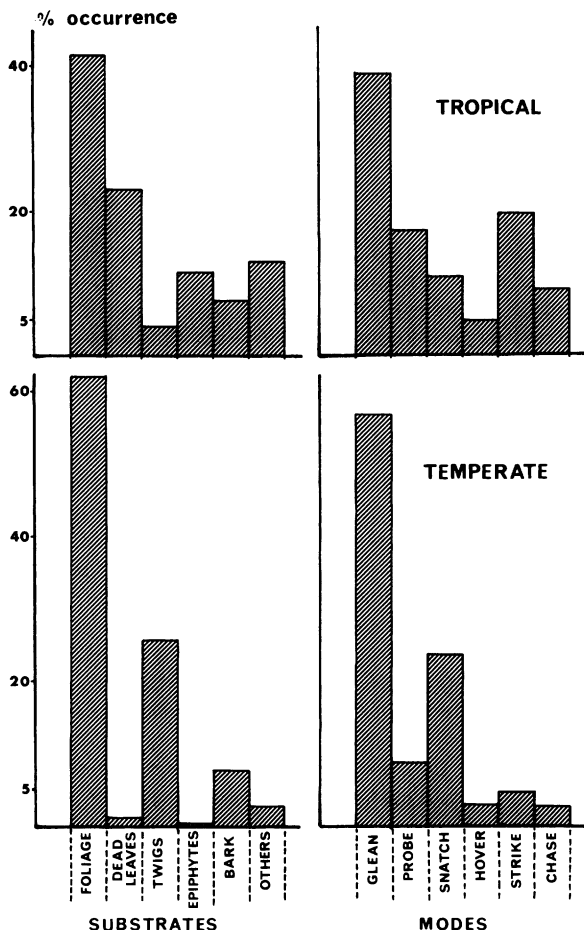
SUBSTRATES   MODES

Fig. 4. Comparative overall frequency of occurrence of foraging substrates and modes of prey capture for tropical and temperate species (see text).

tween solitary birds and members of flocks. The tropical species are either nearly always hunting in multispecies flocks (*Philydor, Thamnomanes, Myrmotherula*) or they are solitary species, rarely if ever joining flocks, but most often moving in pairs. In contrast, true flocking is almost absent in the temperate species during the breeding period (to which I have restricted the study) but again parent birds feeding young are often in view of each other. Within the tropical group, the mean capture rate of the nine species feeding in flocks tends to be higher than that of the six solitary hunting species ($\bar{X} = 0.60 \pm 0.24$ vs 0.42 ± 0.23 capture min^{-1}) but the difference is not statistically significant (U = 13, P > 0.05, Mann-Whitney U test).

Sites and techniques of capture

Birds of the two guilds may be seen from near the ground to the upper canopy. However the mean *foraging heights* of the 10 temperate species are more concen-

trated (7.1 to 14.5 m, ± 2.9 to 5.6) than those of the 15 tropical species (0.9 to 12.5 m, ± 0.4 to 5.8). Within the old forests and the 0–20 m range studied, the former tend also to forage significantly higher (10.1 ± 2.3 m) than the latter (6.9 ± 3.9 m, t = 2.10, P < 0.05, test t, 2 tailed). There is no correlation between this foraging height and the capture rate neither within the groups (r_s = −0.39 and 0.34, P < 0.05), nor within 23 of the 25 species separately.

The main *foraging substrates* (i.e. sites of observed prey captures) were divided into 6 classes (see Methods): green foliage (including curled leaves), dead leaves (in clusters or not), twigs, epiphytes or vines, bark and others (air, litter, spider webs). The use of each category was calculated as $\Sigma p_i/n$ where p_i is the frequency of utilization of a given substrate by species i and n is the number of species in the group (Fig. 4). Temperate species rely much less on dead leaves (1.3 against 22.9%) and epiphytes (0.3 vs 11.3%) than tropical ones (Kolmogorov-Smirnov two sample tests, P < 0.01, 2 tailed). Indeed both hanging dead leaves and epiphytes are usually much more abundant in tropical than in temperate forests. The importance of dead leaves in South American rain forests for some specialized insectivores is wellknown (Remsen and Parker 1984). Compared with a similar volume of green leaves, they have a higher biomass of arthropods, mainly using them as daytime roosts (Greenberg 1987). However foraging in dead leaves, often tied, clustered or curled, is energetically more demanding than searching the foliage superficially. Probing, tearing, thrusting bill or head into dry leaves is also noisy and reduces antipredator vigilance. One of the tropical species (*Myrmotherula gutturalis*) is highly specialized on dead leaves and six others catch more than 25% of their prey there. Yet their overall success rate is not significantly higher than that of other similar species, probably because of the time lost manipulating the leaves or in transit between patches (see also Gradwohl and Greenberg 1984). In temperate forests, the twigs are more exploited (25.9% of all capture attempts, mainly by tits, against 3.9% in the tropical sample).

If the lower foraging success in the tropics comes from a lower prey detectability, one might suppose that, among other adaptations, arthropods are more often under the leaves than on their more exposed upper side. The position of a capture on green leaves could be determined 473 times (all species together). In the tropical forest, 77.6% of the attacks recorded were directed towards leaf undersurface against 38.2% for temperate species. The difference is highly significant (χ_1^2 with Yates' correction = 291.06, P < 0.001). Greenberg and Gradwohl (1980) in a similar neotropical forest estimated that up to 90% of insect prey were taken under the leaves and that at least in the low understory, 70–80% of the arthropods were found on leaf undersides. Birds foraging in the canopy are likely to make a greater use of leaf upper surfaces (pers. obs.).

Foraging modes. Again the proportions of the six main capture techniques are not similarly distributed between the two sets of species (Fig. 4). Gleaning is less frequent and probing, striking and sallying (or chasing) are more often used by tropical than by temperate species. All differences are significant (P < 0.05, Kolmogorov-Smirnov two sample test, 2 tailed). Croxall (1977) explained the higher frequency of hover – or flycatcher – gleaners in lowland rain forest by a larger mean size of leaves and a greater proportion of big insects. Non gleaning techniques which are more prominent in tropical species are also energetically more costly. If, as a rough ranking of energy expenses, the frequencies of glean, snatch, probe, hover, strike and chase were multiplied by a coefficient of 1 to 6 respectively, the mean cost of an average capture would be 54% higher for tropical than for temperate species.

Unfortunately it is not possible to test any correlation between foraging modes or substrates and capture rates because during most individual observations, birds were searching more than one substrate and using more than one capture method. The highest degree of specialization was a 61 to 79% use of gleaning by two tropical and five temperate species or a 62 to 84% use of foliage by six tropical and six temperate species.

Niche breadth. The foraging niche breadth of each species may be calculated using Levins' formula: $B = (\Sigma p_i^2)^{-1}$ where p_i is the frequency of occurrence of each capture technique or substrate use. B here varies from 1 to 6. The mean overall niche breadth tends to be larger in tropical than in temperate species: $\bar{B} = 2.82 \pm 0.69$ vs 2.45 ± 0.78 for capture methods and 2.69 ± 1.01 vs 1.93 ± 0.56 for foraging substrates. The differences are significant (Mann-Whitney U test, 2 tailed: U = 42 and 39 respectively, $P \geq 0.05$).

Discussion

It may seem unwarranted to compare so distantly related species and habitats. However I have tried to control as much as possible for every difference between temperate and tropical data sets. All the species chosen are passerines of similar size, morphological, ecological and behavioural characteristics, belonging to the foliage gleaning insectivore guild, foraging in the low to medium height strata of the most mature types of natural broad leaved forests. All the data have been recorded by the same observer, using the same methods and ranking, only on adult birds during the breeding season. Any bias may thus equally apply to both groups. The only difference is the higher frequency of flocking among tropical species, but flocking is likely to increase the feeding rate of the species involved and thus to strengthen the results.

The sampling was evenly spread over a two-month period in France and a 3.5 month in Guiana. However the breeding period of the temperate forest species may be more synchronous and active than that of the rain forest birds where at any time a higher proportion of individuals is likely to have no young to feed (through delayed breeding or renesting attempts, smaller clutches and more frequent brood losses). Birds feeding young may be easier to find and may have a higher foraging rate than birds hunting only to cover their own requirements. Thus more data coming from the actual nestling phase in France (?) may partly explain an increased mean foraging rate. However only 44% of the temperate birds studied (against 36% for neotropical ones) were obviously feeding young (followed by begging young or carrying prey after capture).

The attack rate measured is an index of how often suitable prey is found. It reflects the searching success more than a true foraging success which would require more information on the percentage of successful attacks, the size, kinds and energy value of prey taken. It may be viewed in terms of maximum gain rate. Since only birds foraging actively and continuously were recorded, their attack rate is correlated with the availability of detectable prey, i.e. capture opportunities, which may be different from true prey abundance. For lack of large samples pertaining to different situations, several factors likely to affect the attack rate were not studied (sex, habitat, vegetation structure, breeding stage, flocking behaviour, season, hour, weather, energy requirements).

There are several conflicting demands upon the time budget of foraging birds such as interference competition, predator vigilance and avoidance of heat stress. Such behaviours were excluded from the sample periods when clearly recognizable (social interactions, rest) but otherwise incorporated into the searching behaviour. The total time spent foraging per day has not been assessed even if it ultimately determines the daily food consumption and hence the bird's energy balance. Still the available daylight period is lower in the tropics (no more than 11 h in the undergrowth against 16 h in temperate forests in June) and the birds exhibit a similar decrease of activity during the middle of the day at both latitudes. This temporal decrease may be related to heat stress as well as to the higher activity (escape behaviour) of insects at that time (Hutto 1981) and hence to a higher cost of hunting. The often greater frequency of rains in the tropics, which inhibit the hunting of forest insectivores (Foster 1974, Kacelnik 1979, pers. obs.) is an additional factor.

The measured attack rates (2–4 min^{-1} for temperate species and < 1 min^{-1} for tropical ones) are consistent with the very few published data: 1.5 to 6 min^{-1}, and sometimes more, for North American warblers (Morse 1968, 1981, Robinson and Holmes 1982, 1984), 3 to 11 on average for several foliage gleaners in Australian eucalypt forests (Cameron 1985, Holmes and Recher 1986), feeding rates to nestlings of up 1 to min^{-1} in

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British tits (Perrins 1979) and conversely 0.54 capture min^{-1} for a brasilian *Hylophylax naevioides* (Willis 1972) or 0.49 to 0.80 for Peruvian *Cacicus cela* (Robinson 1986). Chaurand (1987), using the same technique in a broad leaved forest 150 km west of my French study area, obtained similar rates (on 201 samples from five species). In Guiana (same localities and season), I recorded the attack rates of 35 additional primary forest insectivores during 153 sampling periods (572 min): the overall capture frequency was 0.39 min^{-1}.

In a previous study (Thiollay 1984), at the extreme northern tip of the neotropical forest extension (Tamaulipas, Mexico), intermediate rates were recorded for resident understory warblers and vireos (0.6 to 2.0 capture min^{-1}) whereas the foraging success of similar coexisting North American migrants, although moving higher in the canopy, was 116% greater. This last difference raises the possibility that temperate birds may have higher energy requirements or higher foraging tempos and/or select richer microhabitats.

There were no consistent correlations between hunting method, height or substrate and success rate, at least without taking into account the unknown energy balance between demands and gain. No unusual abundance or scarcity of any prey species in any year or study site was noticeable and likely to account for a significant part of the latitudinal difference observed. Clearings, edges, second growth and upper canopy where the density and conspicuousness of invertebrates (Janzen 1973), as well as the attack rate of insectivores (pers. obs.), may be higher, were not studied.

Most temperate species move more rapidly and thus are likely to encounter prey more often or to make significantly more attacks per unit time than do tropical species. Such a behaviour is rewarding only if conspicuous, non-poisonous, easy to catch and abundant prey are available. Conversely tropical birds are mostly slow searchers that scrutinize or probe substrates more thoroughly or deeply to catch more cryptic or hidden prey. This difference may be an adaptation to a relatively lower food availability in the tropical forest, i.e. either a lower overall prey density, or a lower detectability or a higher diversity (few species allowing specializations and the use of searching images) or both. As a whole, 45% of rain forest arthropods are caught inside clusters of dead leaves, epiphytes or curled leaves against less that 4% in France. Twigs, the only substrate less used in the tropics, have no hiding place and temperate arthropods may be less reluctant to frequent exposed sites.

However the lower attack rates of tropical primary forest insectivores may have other, at least partial, explanations than food accessibility alone. For instance, a *higher antipredator vigilance* may significantly slow down the birds' movements. The predation pressure on adult birds is unknown in both study areas. The overall density of specialized hunters of adult passerines (*Accipiter* spp.) does not seem higher in the Guianan than in the French forests (Thiollay, unpubl.) but the number of potential, occasional predatory species (including snakes and mammals) is definitely much higher in the rain forest. In a subtropical forest of northern Mexico, temperate migrants had both a higher foraging speed and a higher mortality rate from raptors (accounting for all the pluckings found) than residents (Thiollay 1984).

The higher and more stable temperature in tropical forests may result in a lower cost of thermoregulation and consequently *lower energy needs* and food consumption. Indeed, several tropical birds have lower daily food consumptions than similar temperate species (Thiollay 1976). However optimal foraging theory predicts that when they are foraging, birds may forage optimally, i.e. may have a maximum search rate. Any reduction in energy need may be only reflected by a shorter time spent foraging on a daily basis. It is also arguable that, in a high ambient temperature, especially in humid windless undergrowth, birds *avoid heat stress* by reducing their movements or speed and favour less active or expensive foraging behaviours than in cooler environments.

Food resources are obviously more diversified in tropical than in temperate forests and productivity is spread over a longer period. But the overall annual production or even the standing prey biomass may not be higher (Janzen 1973, Karr 1975, Hails 1982, Erwin 1983) and the annual growth rate of the phytomass may even be lower (Klinge et al. 1975, Heuveldop and Neumann 1980). The few studies on insect populations in the Amazonian forest (Penny and Arias 1982, Erwin 1983, Owen 1983), show that the prey biomass of foliage insectivores is not very high and is made up predominantly of small sized or inconspicuous arthropods. Hails (1982) even found during the breeding season an insect biomass ten times higher in Scotland than in Malaysia. Recent detailed studies (Dyrcz 1985, Marcotullio and Gill 1985) show how understory rain forest passerines may be limited by food (up to 90% of daily time budget spent foraging, slow growth and starvation of young). I have performed on each study site 100 sweep net samples of the foliage around 2 m high and found that the abundance and biomass of arthropods were respectively 56 and 69% lower in Guiana (October) than in France (June), the much lower density of caterpillars in the rain forest accounting for most of the difference. The diffuse competition by a larger set of sympatric species may also be more intense in the tropical forest (Keeler-Wolf 1986). Strong seasonal fluctuations of both fruit and insect production are frequently cited in rain forests (see Willis 1976, Leigh et al. 1983, Sabatier 1985). Consequently, the former picture of tropical forests where food was plentiful, or at least unlikely to be a limiting factor, is increasingly questioned. Moreover, periods of food scarcity are often unpredictable in space and time and such a seasonal instability is an additional constraint. The flush of surplus food available to temperate birds for breeding hardly occurs in tropical forests and the lack of a

marked seasonal mortality keeps the tropical populations close to the carrying capacity of the ecosystem.

In the Guianan primary forest, the clutch size is 1 or 2 eggs for most passerines against 4 to 8 in the French mature stands (unpubl. obs. and O. Tostain, pers. comm.) and the breeding cycles are markedly seasonal (see also Miller 1963, Immelmann 1971, Fogden 1972, Karr 1976, Greenberg 1981, Bell 1982, Gradwohl and Greenberg 1983 for other tropical areas). Several theories have attempted to explain the latitudinal decrease of clutch sizes toward the equator (Wagner 1957, Cody 1966, Klomp 1970, Slagsvold 1981, Winkler and Walters 1983). Among them, the food availability hypothesis (Lack 1954, 1968) and its refinements (see Owen 1977, Murphy and Haukioja 1986) is the most often cited and supported by experimental tests or field evidence (Royama 1969, von Haartman 1971, Ricklefs 1977, Møller 1984). It states that food availability is an important proximate constraint, mostly for the laying female (egg formation), during the nestling period (growth rate of young) and even up to the post fledging stage (to maximize the number of surviving offspring). The seasonality and nest predation hypotheses (Skutch 1949, 1985, Ashmole 1961, Ricklefs 1977, Murray 1985) are not inconsistent with Lack's theory and are especially relevant to the situation found in my Guianan study site.

A limited food supply or the difficulty for predators to cope with a great diversity of seasonal, cryptic, hidden or toxic prey may be important determinants of the low reproductive rates in tropical forests. This is supported by many field observations: the long post-fledging dependency of some young passerines and the very low rate of prey deliveries to nestlings (Tostain, pers. comm. in Guiana); the high proportion of daytime spent foraging despite expected lower energy needs (Marcotullio and Gill 1985); the apparent inability of some tropical species to increase their feeding rates to enlarged broods (Simmons 1986); the larger clutch sizes in open tropical habitats, where prey availability is seemingly greater (Lack and Moreau 1965, pers. data); the large clutches of tropical populations when prey density is unusually high (Lenton 1984); the seasonal movements of some rain forest species during periods of food scarcity (frugivores in Guiana). A difference in food quality may also be involved. For instance the higher proportion of caterpillars in the temperate species' diets (energy content, digestibility, accessibility) may be a significant factor.

Low food availability, and associated energy or time costs of foraging, may also influence clutch size indirectly through cost of reproduction and prospect of survival for the adults. Similarly, other factors likely to be significant in the evolution of clutch size (food quality, predation pressure, population demography, nest site, ...) are rarely independent of the capacity of breeding adults to gather enough food at a reasonable cost. Many more investigations are needed to support our preliminary findings, but two traditional views on the rain forest ecosystem must now be questioned: food resources seem to be far from superabundant and their limited availability could be involved in the evolution of low clutch sizes among understory birds.

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