Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*)

Heinz-Ulrich Reyer[1]* and Klaas Westerterp[2]

[1] Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, Federal Republic of Germany
[2] Biomedisch Centrum, Postbus 616, NL-6200 MD Maastricht, The Netherlands

Summary. Energy expenditure of adult Pied Kingfishers was measured with doubly-labeled water. Results were related to reproductive success of parents aided and unaided by helpers. Energetically stressed parents in a colony with poor food supply accepted potential helpers more often than unstressed birds in another colony where food was easily available. This treatment of helpers was reversed in both colonies through experimental manipulation of clutch size and hence energetic stress. Results are discussed in relation to the costs and benefits that helpers incur on the parents' fitness.

Introduction

In recent years several authors have attempted to explain cooperative breeding in birds as an adaptation to ecological conditions (e.g. Brown 1974; Orians et al. 1977; Gaston 1978; Koenig and Pitelka 1981; Emlen 1982, 1984). The critical test for such a hypothesis is to compare inclusive fitness values of conspecifics pursuing different behavioral strategies in identical environments and of those pursuing identical strategies in different environments. Such a comparison is possible in the Pied Kingfisher (*Ceryle rudis*). It was shown previously that males choose the strategy which yields the highest inclusive fitness under the prevailing ecological and demographic conditions (Reyer 1980, 1984). For male breeders this choice means to reject potential helpers (which are always males and therefore also potential rivals) when food conditions are good but to accept them when conditions are too poor for parents to raise all their hatchlings unaided. If birds are to make this ultimately correct decision they require proximate mechanisms which are (1) constantly available and (2) good predictors of fitness, i.e., they must be closely related to current reproductive success and the probability of survival. Energy balance is a likely candidate. Although a negative relationship between energetic stress in one year and survival into the next has only been shown for a few species (Nur 1984), including the Pied Kingfisher (Reyer 1984), current reproductive success in many species is closely linked to energy balance and body condition (Drent and Daan 1980). These in turn depend on environmental conditions, particularly food. The conditions in a given season determine whether a bird will breed at all, how early and how often eggs will be laid, how big the clutch will be, how much food the parents can bring and consequently what the growth and survival rate of the young will be.

It is conceivable that the parents' decision to accept helpers or not also depends on energy balance and body condition. Perhaps a bird could compare the food requirements of the young (as communicated in their begging) to its own feeding capacity and the amount of competition from helpers. This hypothesis combines conclusions from the above mentioned energetic studies with an idea, originally suggested by Orians et al. (1977) and recently modelled by Brown (1982, 1984) and Emlen (1982), namely that parents should accept or reject helpers according to need. We tested this hypothesis by measuring first the daily energy expenditure (DEE) of feeding adult Pied Kingfishers in two ecologically different colonies, using doubly-labeled water. We then related the DEE of parents to their reproductive success, their behavior towards potential helpers and the begging duration of their young under normal conditions. Finally we manipulated clutch size, changing the begging

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* To whom offprint requests should be sent

of young and the energetic stress of parents. We only consider the treatment of "secondary helpers", unrelated to the breeders, and not that of related "primary helpers". The latter apparently do not compete with the breeders for females and were tolerated under all observed circumstances (Reyer 1980, 1984 and in preparation).

Methods

The study was carried out between 1981 and 1983 on two breeding populations at Lake Victoria and Lake Naivasha, Kenya (Reyer 1980). Adult birds who fed nestlings were caught in the late afternoon, weighed and then injected with 0.5–0.8 ml of 18% (excess atom percent) oxygen-18 enriched and 10% deuterium enriched water ($^2H_2^{18}O$). After 1 h of equilibration ca. 60 µl blood was extracted from the wing vein before releasing the bird. Birds were recaptured and weighed, and blood samples taken again 24 h (or a multiple thereof) later. CO_2 production was calculated from the reduction of ^2H and ^{18}O between the first and second sample as described previously (Westerterp and Bryant 1984) and then converted into DEE (kJ) with an RQ value of 0.8 for fish protein on which the birds feed almost exclusively. Additionally, the number, type, and size of fish provided for nestlings by the injected bird was monitored during the whole activity period. The daily food contribution of the $^2H_2^{18}O$-injected bird was calculated from these data as described earlier (Reyer 1984) by using the length-weight relationships in Table 1. In the same way the contributions of all other birds feeding at the particular nest were recorded. From the total amount of food and the known number of nestlings the average energy intake/nestling and day was calculated. The effect of that intake on growth was measured by weighing nestlings before and after the experiment when in the post-absorptive state. Weights were usually taken at 530 h, before the first feed of the day.

The nestlings', hunger was monitored by placing a microphone at the entrance of the nest chamber and connecting it to a tape recorder in the observation hide. Ca. 10 s recordings were made every 5 min throughout the day to determine whether the chicks were begging. Begging duration was expressed as the percentage of recordings with begging, excluding cases in which the nestlings were being fed or had been fed in the previous minute. All the above measurements on adults and young were taken when the nestlings were 5 to 17 days old. In Pied Kingfishers this is the period of linear growth (Reyer, unpublished data). Details of the manipulation experiments will be mentioned with the results.

Results

Energy expenditure and feeding capacity

As the daily energy expenditure of adults increases, the amount of food delivered to nestlings rises in a linear fashion at both lakes but with significantly different slopes (Fig. 1; $P = 0.037$, analysis of covariance; Sokal and Rohlf 1969). Thus, a Lake Victoria bird will achieve a lower feeding contribution than one from Lake Naivasha for the same amount of energy expended. The ecological reasons for this difference include (Reyer 1980): (1)
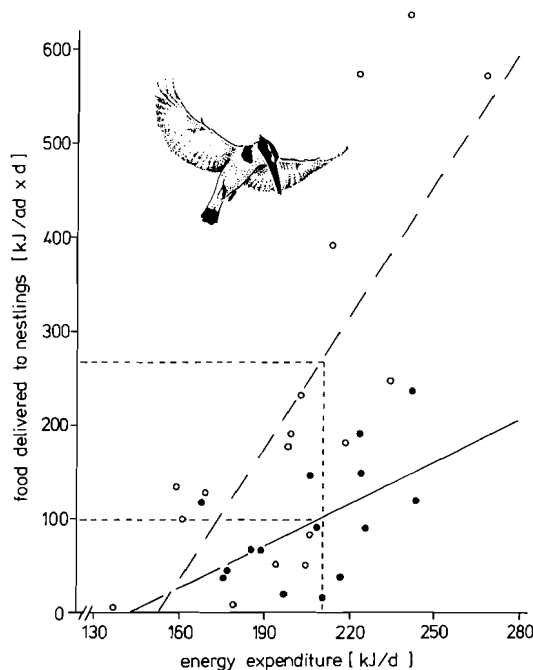

Fig. 1. Amount of food delivered to nestlings (kJ/ad*d) in relation to daily energy expenditure of feeding adults (kJ/d). o − − − o = Lake Naivasha, $y = 4.693\,x - 718.3$; $n = 17$, $r = 0.756$, $P < 0.001$. (●————● = Lake Victoria, $y = 1.485\,x - 209.9$; $n = 15$, $r = 0.545$, $P = 0.036$. ······ = Upper limit of energy expenditure (from Fig. 2) and resulting feeding capacities respectively

a lower energy yield per fish at Lake Victoria which must be compensated for by catching more fish (cp. allometric equations in Table 1), (2) greater turbidity of the water (leading to lower hunting success) and longer distances between fishing grounds and the breeding colony at Lake Victoria resulting in more flying and hovering time per catch.

The ranges and averages of body mass before injection were not significantly different between birds from the two lakes (both medians 76 g; Lake Victoria: interquartile range 72.0–80.0, $n = 15$; Lake Naivasha: interquartile range 70.5–78.5, $n = 17$; $z = 0.566$, N.S., Mann-Whitney U-test, two-tailed).

Birds with a DEE of up to 210 kJ maintain or even increase their body mass (Fig. 2). Above that they increasingly lose mass ($P < 0.001$, Mann-Whitney U-test, one-tailed), as much as 9.2%/day. Thus 210 kJ seems to represent some physiologically determined threshold which cannot be exceeded for prolonged periods without a reduction in body mass. Possible reasons for this reduction will be addressed in the Discussion. Entering the threshold of 210 kJ into Fig. 1, we can predict that on average a pied kingfisher at Lake Naivasha can deliver as much as 267.2 kJ/day without losing

Table 1. Relationship between standard length sl (mm), dry mass M_d (g) and energy content (kJ/g M_d) for cichlid fishes and *Engraulicypris argenteus* (Cyprinidae) from Lake Victoria and for *Tilapia ssp.* (Cichlidae) and *Micropterus salmonides* (Centrarchidae) from Lake Naivasha. r = Pearson correlation coefficient between sl and M_d (sample size = n_1). x and SD = mean and standard deviation of energy content/g M_d as analyzed by bomb calorimetry (sample size = n_2)

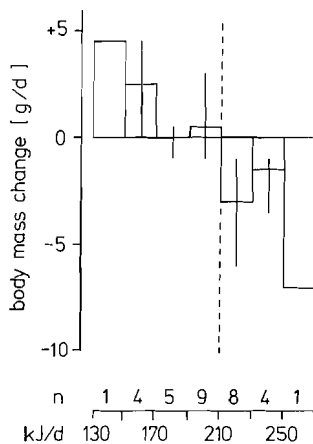| Prey type	Regression	r	n_1	x	SD	n_2
Engraulicypris	log M_d = 0.037* sl − 2.320	0.98	52	19.95	0.61	3
Cichlidae	log M_d = 0.026* sl − 1.461	0.99	95	18.89	0.23	3
Tipapia ssp. + *Micropterus*	log M_d = 0.023* sl − 1.258	0.97	44	19.52	0.96	8

Fig. 2. Medians and interquartile ranges of body mass change (g/d) in feeding adults in relation to their energy expenditure (kJ/d). Data from both lakes combined

Fig. 3. Body mass change (y_m) of nestlings (●————●) and begging duration (y_b) (+---+) in relation to the amount of food received. y_m = 0.124 x − 11.06; n = 22, r = 0.909, P < 0.001. y_b = −0.447 x + 79.06; n = 15, r = −0.830. P < 0.001. Arrows show the average amount of food/day and the average daily change in body mass for a nestling at Lake Naivasha (white arrows) and Lake Victoria (black arrows)

body mass (95% confidence limits: 193.1–341.3). A Lake Victoria bird can only deliver an average maximum of 101.9 kJ/day (70.0–133.7) which is 61.8% less. Some values lie above these thresholds in both colonies. However, days with high food deliveries are regularly followed by days with exceptionally low ones. Although a bird may exceed the predicted thresholds for short periods it apparently does not maintain a higher performance, with concomitant reduction in body mass, for several days or even weeks. We therefore consider the above values to be the "average feeding capacities".

Growth of nestlings

The effect of the different feeding capacities of the two lakes on growth and survival of nestlings is shown in Fig. 3 (data from both colonies combined). The daily body mass change/young is plotted against the average amount of food the nestling receives. One parent at Lake Naivasha has a feeding capacity of 267.2 kJ/parent and the average clutch size at hatching is 4.8 (Reyer 1980 and un-
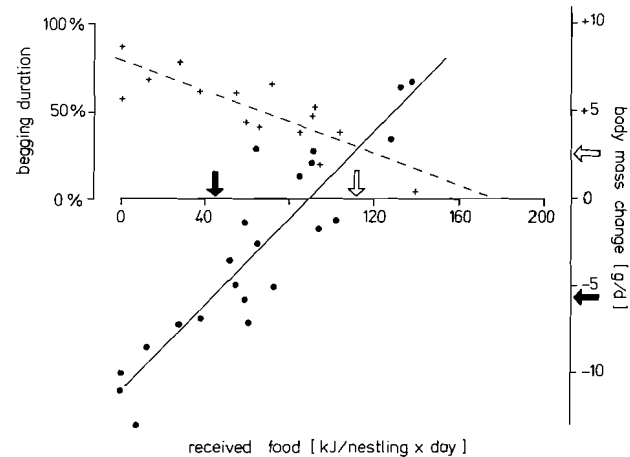
published data). With two parents, each nestling will therefore receive an average of 111.3 kJ/day (= 2*267.2/4.8). According to Fig. 3, this results in a body mass gain of 2.7 g/day (95% confidence limits: 1.1–4.3). Hand-reared Pied Kingfishers of the same age, fed ad lib., showed a mean growth rate of 4.3 g/day (SD = 1.0; based on five birds individually averaged over 7 days within the period of linear growth). Thus, even without helpers, Lake Naivasha parents can guarantee growth of all their young at a rate not too far below that of a nestling under optimal conditions. However, nestlings raised at Lake Victoria by parents alone will receive only 44.3 kJ as each parent has a feeding capacity of 101.9 kJ and the average clutch size at hatching is 4.6. This is unsufficient and will lead to an average body mass loss of 5.6 g (95% confidence limits: −6.8 to −4.4). High competition among nestlings is to be expected and some will survive at the expense of others.

These predictions, based on the energetically limited feeding capacities of adults, are borne out by the results. Unassisted pairs at Lake Victoria loose 61% of their young, mainly due to starvation, as opposed to 19% at Lake Naivasha although both start with a similar number of eggs (probably limited by incubation constraints). While one and two helpers at Lake Victoria can reduce losses to 22% and 0% respectively, pairs with helpers as Lake Naivasha do not fledge significantly more young than those without (Reyer 1980, 1984, unpublished data).

Begging of nestlings

The begging of young probably tells adults whether they are receiving sufficient food and thus whether helpers are needed. It has a clear influence on the adults' feeding patterns. Parents resting in the colony were regularly observed approaching the nest entrance and either resuming rest when the begging response was soft or immediately flying to the lake when it was intense.

Daily duration of begging decreases significantly as food supply increases (Fig. 3). Consequently, the average begging duration at Lake Victoria is longer than at Lake Naivasha. It appears possible that the differences in the demands of the nestlings and the energetic stress on parents (Fig. 1) between the two colonies were the proximate mechanisms responsible for the different treatment of helpers at Lake Victoria and Lake Naivasha.

Manipulation experiments

This hypothesis was further tested by reversing the energetic stress and begging duration in the two colonies through manipulation of clutch size and by comparing the treatment of helpers under normal and manipulated conditions. A potential helper was labeled "rejected" when his attempts to feed adults and nestlings of a pair were aggressively prevented by the male breeder of that particular pair. Helpers which were greeted and allowed to feed were labeled "accepted". A more detailed description of the respective behavior patterns is given by Douthwaite et al. (in press). Observations were confined to male breeders because it is they who compete with male helpers over the scarce females. Females proved to tolerate helpers much more readily (Reyer, unpublished data).

In unmanipulated conditions, the male breeder's "decision" whether to accept a potential helper or not is usually made within the first 7 days
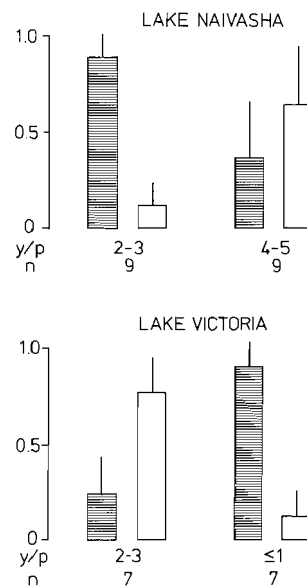

Fig. 4. Proportions of encounters in which mated males (n) attack (hatched bars) or greet (white bars) potential secondary helpers. Top: Lake Naivasha; bottom: Lake Victoria; left: normal clutch size (2–3 young/parent); top right: increased clutch size (4–5 young/parent); bottom right: reduced clutch size (≤ 1 1 young/parent). The two bars of each graph add up to 1.0. Means and standard deviations are given

after hatching (Reyer, unpublished data). Birds which were not tolerated by day 10 were not accepted later either. The following data come from breeders with nestlings older than 10 days.

All potential helpers had been rejected before hatching (Reyer 1984, unpublished data). At Lake Naivasha 88% of the breeding males ($n=25$) continued to reject them under normal conditions (2–3 young/parent) as opposed to 0% ($n=31$) at Lake Victoria ($\chi^2 = 44.9$, $P < 0.001$). Then some clutches at Lake Naivasha, with 13–22-day-old nestlings, were experimentally increased to 8–10 young (i.e. 4–5 nestlings/parent), putting the parents into a position similar to that of Lake Victoria birds: they could no longer provide enough food (59.4 kJ/ young; Figs. 1 and 3). Now only 20% of the pairs ($n=10$) rejected potential helpers. This differs significantly from normal conditions ($P < 0.001$, Fisher test, one-tailed). The reverse experiment was equally conclusive. When clutch size at Lake Victoria was reduced to 1–2 (i.e. 0.5–1 nestling/parent and 135.9 kJ/young) potential helpers were rejected in 87.5% of the cases ($n=8$), also different from normal conditions ($P < 0.001$). These differences do not result just from the fact that birds which spend more time in getting food have less time to chase away potential helpers. Such an ex-

planation can be ruled out by the results from Fig. 4 which show the proportion of encounters in which the mated male either attacks or greets the potential helper. Attacks prevailed at Lake Naivasha and greeting at Lake Victoria when clutch size was normal. However, when it was increased, Lake Naivasha birds switched from attacking helpers to greeting them ($P=0.01$, Wilcoxon-test, one-tailed), whereas in Lake Victoria birds with experimentally reduced clutch size attacking prevailed over greeting ($P<0.01$, Mann-Whitney U-test, one-tailed).

The application of the Wilcoxon-test to Lake Naivasha data and of the U-test to Lake Victoria results, reflects the slightly different experimental design in the two colonies. At Lake Naivasha some birds were observed before and after increasing their clutch sizes. Thus, the data from manipulated clutches represent a subset of the data from the normal clutches. At Lake Victoria normal and manipulated clutches represent independent samples. Here, clutch size was already reduced 1–2 days after hatching, before any helper had been accepted. This differential design resulted from observations of undisturbed groups, showing that once a helper has been accepted, he will remain accepted, independent of how the brood size develops. Experimental reduction of clutch size in two pairs with accepted helpers confirmed these observations.

In summary: (1) male breeders reject potential helpers when the parents can raise all their young alone, (2) they switch from rejecting to accepting when the nestlings food requirements exceed the parents' feeding capacities, but (3) once a breeder has accepted a helper, he does not later reject him if the required feeding effort decreases.

The influence of the begging of the young on the treatment of helpers was tested separately. Loudspeakers were hidden close to the nest entrances of two pairs at Lake Victoria both of which had two young (12–15 days old) and had rejected potential helpers so far. Begging recordings were played throughout the day for 4 min followed by 1 min of silence (80% begging duration). At first, both pairs' feeding frequencies were higher than those of the day preceeding the experiment. However, they soon returned to normal and after 2 days had still not accepted helpers. After entering the nest the parents probably received compensating behavioral stimuli from their young which were well fed during this experiment. The nestlings may even not have been gaping on occasion, as parents seemed to leave the nest carrying fish more often than usual.

Discussion

Energy is often considered one of the most important factors in shaping cooperative breeding (Brown 1982, 1984), territoriality (Gill and Wolf 1975; Ewald and Carpenter 1978; Davies and Houston 1981), group foraging (Jarman 1974; Krebs 1974; Krebs and Cowie 1976), and other social behaviors (Pulliam et al. 1974; Caraco 1979; Caraco et al. 1980). However, quantitative energy budgets are usually only measured in relation to an individual's size, age, sex, thermal environment or activities (see Walsberg 1983 for a review) and rarely in a social context. This discrepancy between proposed importance and actual analysis of energy arises mainly from the difficulties of recording natural social behavior under laboratory conditions and measuring energy budgets precisely under field conditions. The development of the doubly-labeled water method (Lifson and McLintock 1966) has overcome the latter difficulty even within complex social situations like cooperative breeding.

The critical DEE beyond which Pied Kingfishers lose body mass is 210 kJ (Fig. 2). This average value ignores individual variations in body mass and so do the calculated regressions between parental feeding capacity and energy expenditure (Fig. 1). Such variations could be important (a) because light individuals need less energy than heavy ones (cp. allometric equations in Aschoff and Pohl 1970) and (b) because weight loss may be an adaptive strategy (e.g. Norberg 1981). Argument (a) could be held responsible for the observed difference in energy expenditure between the two lakes, if Lake Naivasha birds were lighter than Lake Victoria birds. This, however, did not apply (see Results). Argument (b) seems to find support from the fact that the critical DEE of 210 kJ is 22% lower than expected for a 76 g bird on metabolic grounds (Kirkwood 1983). We are not able to tell whether a Pied Kingfisher parent is unable to expend more than 210 kJ without losing body mass or whether he "chooses" to reduce his mass to save energy. This, however, does not alter the notion that body mass change is related to energy expenditure and that there is a critical DEE which demands mass loss.

The threshold of 210 kJ/day is almost identical to the value predicted for a bird its size from the 4*BMR (basic metabolic rate) regression line which Drent et al. (1978/1979) calculated for 31 bird species. The majority of these were fish-eaters like the pied kingfisher. In most bird species investigated so far, 4*BMR seems to represent the upper limit of energy expenditure which cannot be ex-

ceeded for prolonged periods without a decline in body condition (Drent and Daan 1980; Westerterp and Drent, in press). Such a decline can have both short-term effects on present and long-term effects on future reproduction. There is a significant negative correlation for the Pied Kingfisher and a few other species between amount of feeding in one year and survival into the next (Nur 1984; Reyer 1984). Thus, energy expenditure is indeed a currency for fitness costs, a reliable proximate indicator of ultimate reproductive success.

Selection will consequently favor thresholds of energy expenditure which maximize current reproductive success with minimal costs for the residual reproductive value. Where for ecological reasons there is a danger of crossing these thresholds, behavioral traits which reduce energy expenditure will be developed. Recruitment of helpers under poor food conditions is one such trait. However, the benefits of reduced energetic stress and improved reproductive success through helpers must be weighed against the costs which Pied Kingfisher helpers can impose on breeders. These are mainly from competition for their mates (Reyer 1984, in preparation; Reyer et al., in preparation). Male surplus (and consequently competition for females) is similar in both colonies but benefits from helpers differ (Reyer 1980). Thus the high reproductive success and low DEE of parents at Lake Naivasha should shift the outcome of the breeder-helper conflict towards rejection of helpers, whereas the poor reproductive success and high DEE of parents at Lake Victoria should favor acceptance. This indeed happens under normal conditions. When conditions in the two colonies were reversed by experimental manipulation of clutch size, the parents' behavior towards potential helpers was also reversed.

Clutch size could not be manipulated without a corresponding change in time budget. Thus time may appear as likely a limiting factor as energy. The limits could arise from the need to save time for nest-guarding, plumage-maintenance and other important activities (Walsberg 1983). However, even the most active feeders without helpers spent plenty of time "loafing" away from the colony (Reyer and Westerterp, in preparation). Moreover, the breeding season of Pied Kingfishers in other areas coincided with low wind velocities and low water turbidities (Whitfield and Blaber 1978). These conditions favour hunting from a perch rather than by hovering flights (Douthwaite 1976), which saves energy but increases the time/catch ratio (Reyer, unpublished data). We therefore consider differences in energy expenditures between the two colonies to be more important for the differential treatment of helpers than differences in time expenditures. This does not imply any statement about the precise physiological mechanism. We do not pretend that a parent actually monitors his energy state and uses variables such as fat reserves or CO_2-production as the immediate cues to vary his treatment of helpers. Our results only show that the decision between acceptance and rejection is somehow influenced by the energy budget.

Energy expenditure also differs considerably between populations and individuals of other species (Bryant and Westerterp 1983; Karasov and Anderson 1984; Westerterp and Drent, in press). Additionally, intraspecific variation can be seen in the behavior of cooperative breeders and other social animals (Emlen 1984; Lott 1984). Therefore the causal relationship between energy expenditure and social behavior reported in this paper may hold for many more species. This is not a new idea. Several authors have already emphasized that cooperative breeding is shaped by ecological constraints such as habitat saturation, food supply, lack of sexual partners or environmental harshness leading to energetically intensive parental investment which can be reduced helpers (Brown 1974, 1982, 1984; Orians et al. 1977; Brown et al. 1978; Gaston 1978; Stallcup and Woolfenden 1978; Vehrencamp 1979; Koenig and Pitelka 1981; Emlen 1982, 1984; Riedmann 1982). However, they did not measure energy expenditure and usually considered only ultimate consequences. This is the first attempt to our knowledge that also deals with the proximate mechanisms by incorporating quantitative measurements of DEE under normal and manipulated field conditions. We feel that this approach will prove useful in many areas of social behavior.

version of the manuscript which was transferred from German English into British English by L. Gardiner, illustrated by D. Schmidl, and typed in its final version by T. Natoli. We are afraid that the cost/benefit ratio for all these unrelated helpers was much worse than for the authors.

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