

The Loading Effect in Central Place Foraging Wheatears (*Oenanthe oenanthe* L.)

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Received February 15, 1982 / Accepted August 12, 1982

Summary. The behaviour of five adult wheatears (*Oe. oenanthe*) delivering prey (maggots and mealworms) from artificial patches to the nestlings was studied. The existence of a so-called loading effect was confirmed. Handling times for subsequent prey items increased with the number held in the beak, which led to a decrease in collecting rates with patch time and, in most cases, to positively accelerating loading functions when collecting times for prey items are plotted as a function of load size. All birds seemed to become more efficient at loading prey in the experimental patches during the course of the nestling period. Loading functions for maggots and mealworms were slightly different. When forcing the birds to visit several cups (only one item in each cup) and remove a layer of moss before reaching the prey (low-density patches), all birds took fewer prey and two of them stayed longer in them than in high-density patches (one cup filled with prey items). This was due to an increase in search times with the number of prey held in the beak.

From knowledge of the loading functions and travel times to the nest, it is possible to predict the optimal load sizes according to a mathematical solution of the delivery rate model of Orians and Pearson (1979). By transforming collecting and travel times to energy expenditures, it is also possible to derive predictions from an energy efficiency model (maximizing energy delivery per unit energy expended in a round-trip). The observed average load sizes did not differ significantly from those predicted by the delivery rate model, but they were significantly smaller in all cases than those predicted by the energy efficiency model. For birds feeding nestlings, it may be more important to sacrifice efficiency in energy expenditure in favour of greater delivery rates, thereby maximizing the growth rate of the young.

Introduction

Central place foraging models (Andersson 1978; Orians and Pearson 1979; Schoener 1979) deal with the behaviour of animals that deliver food items to some den, cache or nest instead of consuming them where found. These models assume that the rate of energy delivered to this central place should be maximised, if foraging behaviour is to be optimal. Similar assumptions are at the core of other optimization models dealing with other types of foraging behaviour (for a review, see Pyke et al. 1977; Krebs 1980).

Orians and Pearson (1979) developed a model dealing with animals that can carry more than one food item at a time, the so-called multiple-prey loaders. They suggested that for these animals the collecting rate of prey items would decrease with time spent in a patch, not only because of prey depletion, but also because the more prey items the predator has to hold, the more difficult it will be for him to capture and handle new ones. It would therefore not always be advantageous for a predator to take the maximum number of prey that it could possibly transport to the central place, as would be the case if the number of items collected increased linearly with time. This has been called the loading effect (Kramer and Nowell 1980). The assumption of negatively accelerating loading functions gives rise to both qualitative and quantitative predictions concerning the optimal load sizes and optimal collecting times in patches in relation to travelling time to the central place and to patch quality. Orians and Pearson (1979) considered the maximization of energy delivery per unit time spent in each round trip. However, travel may require more energy per unit time than foraging in a patch. In that case, the foraging animals may maximize energy delivery to the central place per unit energy expended in a complete round trip

(Kramer and Nowell 1981; Tinbergen 1981; Giraldeau and Kramer, in press).

During the last few years there has been a growing interest in testing the predictions of central-place foraging models (Jenkins 1980; Kramer and Nowell 1980; Andersson 1981; Killeen et al. 1981; Tinbergen 1981; Martindale 1982; Giraldeau and Kramer, in press). Carlson and Moreno (1981) tested two qualitative predictions of the Orians-Pearson model for multiple-prey loaders with wheatears (*Oenanthe oenanthe* L.) feeding their young in the nest. In the present quantitative study of wheatears delivering prey to nestlings, we specifically address the following questions:

1. Is there a loading effect for these birds? If so, what produces this effect?
2. Does prey collecting change during the nestling stage and, if so, what produces these changes?
3. Are loading functions different for different prey types?
4. How does patch quality affect loading behaviour?
5. Are the parents maximizing food delivery to the nestlings per unit time or per unit energy expended in a complete round trip?

Materials and Methods

The field experiments were carried out in an open pastureland south of Uppsala, central Sweden. For a description of the study area, see Carlson and Moreno (1981). The study was conducted in May and June 1981. The subjects of the experiments were two pairs of wheatears and the male from a third pair in three adjacent territories. The female of the third pair did not visit our experimental patches. All experiments with pairs were concluded before the fledging of the first young (15 days after hatching) and were carried out early in the morning when parents were likely to maximize prey delivery to the nestlings.

Several days before hatching we presented the birds with plastic cups filled with mealworms (larvae of *Tenebrio molitor* L.) and maggots (larvae of *Calliphora* flies) near the nest to accustom the birds to the experimental set-up. Some of the cups were covered with a layer of moss. The birds soon fed readily from the cups and also, if necessary, removed the moss layer to take the prey hidden under it. During the experiments we offered the same prey items in plastic cups distributed around stones, which the birds had used before as hunting perches. There was only one experimental patch in each territory. Travelling times were measured with a stop-watch from the moment of leaving the experimental patch to the moment of landing next to the nest.

High-prey density patches consisted of 2 plastic cups filled with either maggots or mealworms. Low-prey density patches consisted of 20 cups regularly arranged around the stone (average distance between cups: 0.9 m), with one maggot in each and layers of moss covering them completely. The birds had to remove the moss layer before taking the prey in each cup and

then move to another cup (average time in seconds between cups and SD for all individuals: 2.4 ± 2.0 , $n=125$). Plastic cups were always placed at the same locations in the experimental patches. Only one experimental set-up was presented at a time. Mealworms were offered only to Pair I during days 10–12 after hatching date, while low-density patches were offered to both pairs during days 6–10. We alternated both experimental set-ups during the days the prey-density and prey-type experiments were performed.

The birds were observed with a telescope (25×) from a place where both the experimental patch and the nest were clearly in view. When a bird landed in a patch, all observations were dictated continuously into a tape recorder as they occurred. The following events were recorded: time of day, individual, type of experimental set-up and all behavioural events occurring between arrival at and departure from the patch. The tapes were later played back together with a running stop-watch to determine durations of all events to the nearest 0.1 s. Handling time for each prey item was defined as the time elapsing from picking up the prey from the cup until the bird ceased to beat it against some object or manipulate it with the beak. Collecting times for prey items were defined as the time elapsing from the landing of the bird on the experimental patch until the prey item in question was held in the beak without more handling. If the bird started to feed, collecting times were taken from the moment when it picked up the first subsequent prey to be loaded. We have not included self-feeding times in the collecting time calculations, as they were usually short due to the low average number of prey eaten per round trip (Table 1). Search times were defined as those periods spent performing all activities at a cup in low-density patches, before picking up the prey. Collecting times in these patches thus included search times at every cup. There were no search times in high-density patches. We have only used round trips in which the birds visited the experimental patches exclusively and then directly returned to the nest. The observations were always interrupted before the birds had taken half of the available prey in a patch, the cups then being refilled. The birds seemed not to be affected by our presence when visiting the experimental patches.

We have treated separately the data from high-density patches of maggots for the early (2–8 days after hatching) and late (9th day after hatching until fledging date) parts of the nestling period to look at the changes in the prey-collecting behaviour of the parents as the nestlings aged. To calculate the loading functions, we have plotted collecting times as a function of load size, due to the discrete character of the load size variable. We should therefore expect a positive acceleration of the loading functions if a loading effect exists. In the original model (Orians and Pearson 1979) and later papers (Kramer and Nowell 1980; Killeen et al. 1981; Giraldeau and Kramer, in press), load size is considered as the dependent variable and the loading functions are thus negatively accelerating. However, the present way of estimating the loading functions does not change anything substantial in the model and leads also to precise predictions. The shape of the loading functions was determined for each individual, time period and experimental set-up. Linear, power and exponential functions and second-degree polynomials were fitted to the data, and the model with the highest r^2 value was chosen to generate predictions. A decline in instantaneous collecting rate (no. of prey collected/collecting time) with respect to patch time was used to confirm the positive acceleration of the loading functions. For that end, correlations between collecting rates and collecting times for each prey item were calculated.

Knowing the loading function which best fits the data, it is possible to predict the optimal load size (L) from travel time

Table 1. Average number (\pm SD) of prey items consumed by the parents at each visit to the experimental patch and the average time (\pm SD) spent eating for each individual, prey density and prey type. Parentheses enclose the no. of round-trips used. The differences in n values are due to cases when the moment of landing was missed or when it was not possible to determine the number of prey consumed

| | Male I | Female I | Male II | Female II | Male III |
|--------------------------|------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| High-prey density | | | | | |
| No. of prey | 1.0 \pm 1.5 ($n=74$) | 1.2 \pm 1.9 ($n=28$) | 0.6 \pm 1.1 ($n=63$) | 1.4 \pm 2.0 ($n=27$) | 2.1 \pm 2.1 ($n=15$) |
| Time (s) | 1.6 \pm 2.8 ($n=60$) | 1.6 \pm 3.0 ($n=18$) | 1.3 \pm 1.8 ($n=52$) | 1.2 \pm 2.2 ($n=25$) | 8.2 \pm 4.8 ($n=7$) |
| Low-prey density | | | | | |
| No. of prey | 0.7 \pm 1.6 ($n=35$) | 0.3 \pm 0.7 ($n=20$) | 0.8 \pm 1.7 ($n=28$) | 0.9 \pm 1.6 ($n=9$) | |
| Time (s) | 6.8 \pm 21.5 ($n=34$) | 2.4 \pm 5.8 ($n=21$) | 4.7 \pm 6.7 ($n=40$) | 3.9 \pm 7.3 ($n=7$) | |
| Mealworms | | | | | |
| No. of prey | 0.5 \pm 1.2 ($n=28$) | 0.2 \pm 0.4 ($n=21$) | | | |
| Time (s) | 0.4 \pm 0.8 ($n=28$) | 0.5 \pm 1.1 ($n=22$) | | | |

(T) alone. The following mathematical analysis is only valid, of course, for positively accelerating functions. Energy obtained per unit time (E) is:

$$E = \frac{L}{T + f(L)}, \quad (1)$$

where $f(L)$ is collecting time as a function of load size. Deriving E with respect to L , we obtain the following equation:

$$T = L^* f'(L^*) - f(L^*) \quad (2)$$

where $f(L^*)$ and $f'(L^*)$ are the loading function, and the derivative evaluated for L^* , the optimal load size. L^* can be obtained from Eq. (2) by iteration. Giraldeau (1981) has derived a similar equation for predicting optimal patch time, when load size is plotted as the dependent variable. For the special case of power functions,

$$E = \frac{L}{T + aL^b} \quad (3)$$

Deriving again E with respect to L , we obtain

$$L^* = \left[\frac{T}{a(b-1)} \right]^{1/b}. \quad (4)$$

The predicted and observed loads in each case were compared statistically using a two-tailed Wilcoxon signed-ranks test (Siegel 1956). We calculated the energy expenditure for sitting or standing (when feeding in high-density patches) as $2 \times$ BMR, for active foraging (when feeding in low-density patches) as $3 \times$ BMR and for flight to the nest as $9 \times$ BMR (Cowie 1977; Zach 1979). The BMR of a 20-g passerine was estimated as 0.08 cal/s, according to Kendeigh et al. (1977). Collecting times and travel times were transformed to energetic expenditures according to these estimations, and the same graphical and mathematical analysis as before was applied to obtain the predicted load sizes according to the energy-expenditure model.

The data for ANOVA and t -tests were subjected to logarithmic transformation ($\log(x+1)$). Means are presented with standard deviations; the tests are two-tailed.

Results

The Loading Effect and Changes During the Nestling Period

Collecting time was a positively accelerating function of load size in high-prey density patches of maggots in all but two cases (Fig. 1). The power model gave the highest fit in 6 of 9 cases, while the r^2 values for the linear functions were the lowest in 7 out of 9 (Table 2). The loading curves rise much more steeply during the first period (Fig. 1), meaning that the birds achieved a higher loading efficiency in our experimental patches after the first week. Instantaneous collecting rates decreased continuously while the birds loaded maggots in the patches (Fig. 2), the decrease being more marked during the first 20 s spent in the patch. Collecting rates were systematically higher for the first period (Fig. 2).

Handling times increased with the number of prey already taken (Fig. 3) except for female II. She did not show any significant trend. Data for this individual are very scarce. Average handling times were significantly longer for the first four prey taken during the first than during the second period (ANOVA for all individuals, $P < 0.001$). This again shows an increase in loading efficiency from the first to the second part of the nestling stage. As handling times constitute a large proportion of collecting times in the patch (mean handling times on average make up 74%, range 47%–98%,

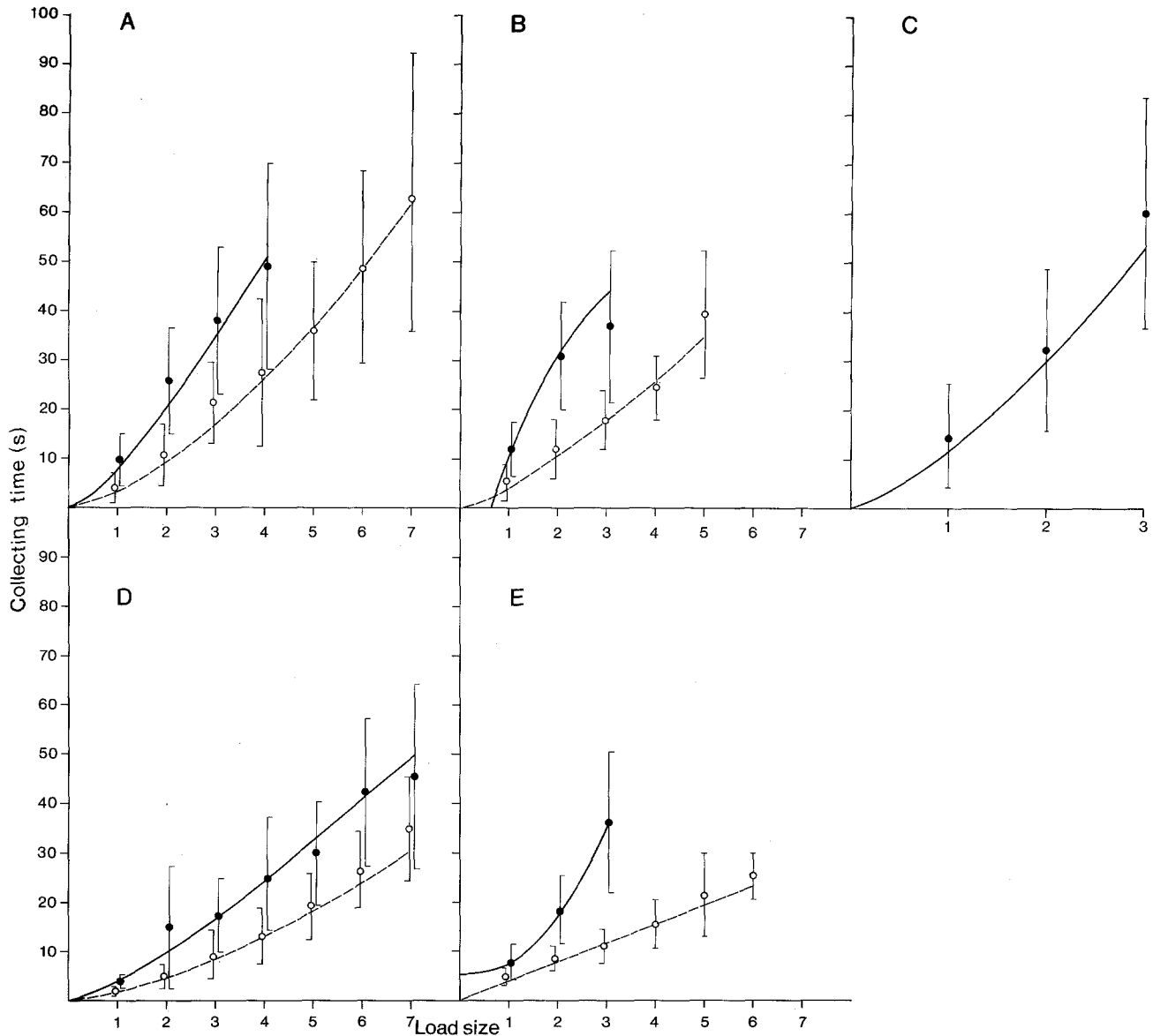


Fig. 1. Loading curves in high prey density patches of maggots for male I (A), female I (B), male III (C, data for the first period only), male II (D) and female II (E), for the first period (solid lines) and second period (broken lines). Means and standard deviations of collecting times for all prey taken according to their ordinal number in prey capture sequences are shown for the first (black dots) and second period (white dots). Values of n are number of round-trips observed. Note the different scale on the abscissa of graph (C). Loading functions are: A Period I, $y = 8.59x^{1.29}$, $n = 55$; Period II, $y = 3.22x^{1.52}$, $n = 22$. B Period I, $y = -14.04 + 29.37x - 3.39x^2$, $n = 11$; Period II, $y = 4.17x^{1.32}$, $n = 17$. C Period I, $y = 11.82x^{1.37}$, $n = 15$. D Period I, $y = 4.06x^{1.29}$, $n = 33$; Period II, $y = 1.76x^{1.46}$, $n = 47$. E Period I, $y = 5.45 - 1.57x + 3.97x^2$, $n = 13$; Period II, $y = 4.24x^{0.95}$, $n = 7$

of the mean collecting times for each prey item), the increase in handling times shown in Fig. 3 should lead to the positively accelerating loading functions depicted in Fig. 1. The negatively accelerating polynomial functions for female I, 1st period, and female II, 2nd period, are really difficult to explain, considering the data for these individuals and periods presented in Figs. 2 and 3.

Differences in Loading Rates for Different Prey Types

Loading functions for mealworms and maggots during the same three days were compared (Fig. 4). The best fit for both prey types was obtained with the power model, while the linear gave the poorest fit in 3 out of 4 cases (Table 2). The loading curve

Table 2. *r*-values for all collecting time – number of prey regressions according to linear-, power-, exponential- and second-degree polynomial models. In parentheses are number of collecting times recorded

| | Linear | Power | Exponential | Polynomial |
|--------------------------|--------|-------|-------------|------------|
| Nestling age comparisons | | | | |
| Period I | | | | |
| Male I (162) | 0.53 | 0.60 | 0.55 | 0.54 |
| Female I (27) | 0.47 | 0.48 | 0.44 | 0.64 |
| Male II (158) | 0.49 | 0.70 | 0.61 | 0.50 |
| Female II (15) | 0.66 | 0.67 | 0.67 | 0.68 |
| Male III (41) | 0.54 | 0.59 | 0.58 | 0.55 |
| Period II | | | | |
| Male I (111) | 0.64 | 0.76 | 0.67 | 0.65 |
| Female I (73) | 0.69 | 0.78 | 0.75 | 0.71 |
| Male II (173) | 0.77 | 0.86 | 0.84 | 0.62 |
| Female II (69) | 0.64 | 0.73 | 0.70 | 0.68 |
| Prey-type comparisons | | | | |
| Mealworms | | | | |
| Male I (67) | 0.58 | 0.73 | 0.72 | 0.59 |
| Female I (50) | 0.69 | 0.76 | 0.74 | 0.69 |
| Maggots | | | | |
| Male I (91) | 0.60 | 0.74 | 0.69 | 0.60 |
| Female I (64) | 0.67 | 0.75 | 0.63 | 0.71 |
| Prey-density comparisons | | | | |
| High-prey density | | | | |
| Male I (44) | 0.74 | 0.80 | 0.70 | 0.75 |
| Female I (28) | 0.59 | 0.70 | 0.66 | 0.60 |
| Male II (93) | 0.74 | 0.84 | 0.77 | 0.76 |
| Female II (24) | 0.66 | 0.61 | 0.60 | 0.64 |
| Low-prey density | | | | |
| Male I (107) | 0.36 | 0.54 | 0.39 | 0.46 |
| Female I (98) | 0.52 | 0.56 | 0.52 | 0.55 |
| Male II (102) | 0.65 | 0.83 | 0.75 | 0.66 |
| Female II (17) | 0.63 | 0.35 | 0.45 | 0.65 |

for mealworms of the female rose faster with the number of prey taken than that for maggots, while for the male the difference was very slight. Collecting rates for mealworms decreased continuously with patch time, and for the female the decrease was faster than for maggots (Fig. 2). We compared the loads of both prey types taken by the two individuals during the same 3 days. The male took on average 5.7 ± 1.4 maggots and 2.7 ± 0.7 mealworms and the female 5.1 ± 1.5 maggots and 2.2 ± 0.9 mealworms. The differences were significant for both individuals (ANOVA, $P < 0.001$). Both individuals took the same average load of maggots, but the male took significantly more mealworms than the female (ANOVA, $P < 0.02$). The maximum observed load of mealworms was 4 as compared to 8 for maggots. Handling times for mealworms rise linearly with the number of prey already taken, and faster than handling times for maggots (Fig. 5). Average handling times are also

significantly higher for mealworms than for maggots (ANOVA for both individuals, $P < 0.02$).

The Effect of Prey Density

Collecting time was a positively accelerating function of load size in patches of both prey densities, except for female II, high density (Fig. 6). The power functions gave the highest fit in 6 of 8 cases, while the linear model gave the lowest in 5 of 8 cases (Table 2). Collecting times increased much faster in low-prey density than in high-prey density patches (Fig. 6). Collecting rates in low-density patches decreased continuously with patch time and were systematically lower than for high density, second period (Fig. 2). All birds took significantly less prey in low-density patches (Table 3), and female I and male II stayed significantly longer in them (Table 3). Both males took significantly more prey than their mates (pair I – high

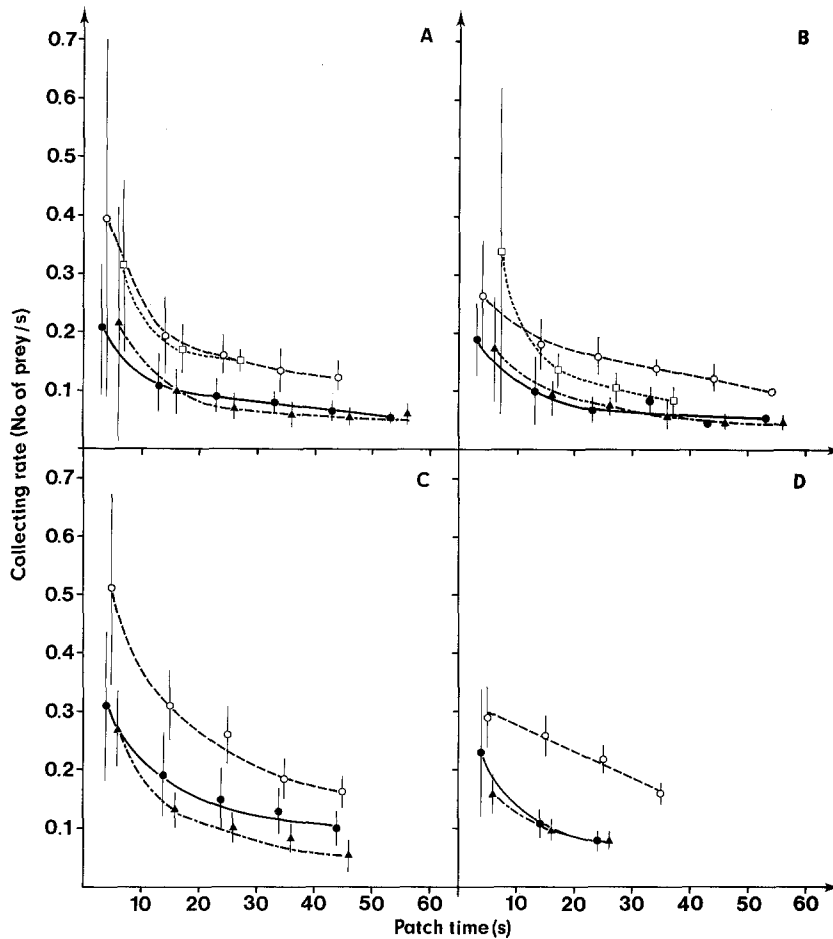


Fig. 2. Collecting rates (no. of prey collected/s) in relation to patch time (self-feeding time excluded) for male I (A), female I (B), male II (C) and female II (D). Means and standard deviations of collecting rates are shown for the collecting time data grouped by 10-s intervals. 1st period = black dots, 2nd period = white dots. Mealworms = white squares, low density = black triangles. Lines are fitted by eye. Correlation coefficients are:

| | | |
|----------|-------------|--------------------------|
| A | Period I | $r^2 = -0.34, P < 0.001$ |
| | Period II | $r^2 = -0.28, P < 0.001$ |
| | Mealworms | $r^2 = -0.63, P < 0.001$ |
| | Low density | $r^2 = -0.22, P < 0.001$ |
| B | Period I | $r^2 = -0.39, P < 0.001$ |
| | Period II | $r^2 = -0.40, P < 0.001$ |
| | Mealworms | $r^2 = -0.53, P < 0.001$ |
| | Low density | $r^2 = -0.15, P < 0.02$ |
| C | Period I | $r^2 = -0.37, P < 0.001$ |
| | Period II | $r^2 = -0.23, P < 0.05$ |
| | Low density | $r^2 = -0.79, P < 0.001$ |
| D | Period I | $r^2 = -0.62, P < 0.05$ |
| | Period II | $r^2 = -0.42, P < 0.01$ |
| | Low density | $r^2 = -0.66, P < 0.001$ |

density $t = 2.05, P < 0.05$; low density $t = 2.84, P < 0.05$; for pair II, high density NS; low density $t = 2.84, P < 0.01$, and male I stayed significantly longer in high-density patches than the female ($t = 2.07, P < 0.01$).

We compared the search times for the first three prey taken by both members of pair I and male II in low-density patches (Table 4), as the data for female II and for more than three prey for all individuals are too scarce to be relevant. For two individuals, search times increased significantly from the first to the third prey (Table 4), but for male I search times for the third prey were significantly lower than for the second prey (Neumann-Keuls multiple range test). These results suggest that the number of prey already collected reduced searching efficiency in the experimental patches.

Optimal Load Sizes

Travel times were calculated as the average for each individual of all recorded flight times to the

nest multiplied by 2 (in seconds, male I: $14.6 \pm 3.3, n = 118$; female I: $15.4 \pm 3.4, n = 38$; male II: $13.5 \pm 0.7, n = 45$; female II: $13.6 \pm 1.1, n = 28$; male III: $12.4 \pm 1.8, n = 24$). By using these values in Eq. (2) for the two cases of polynomial functions and in Eq. (4) for power functions and the obtained loading functions (Figs. 1, 4 and 6), we can estimate the optimal load sizes for each individual, prey type and prey density (Fig. 7). In the cases of linear or negatively accelerating functions, the model predicts the maximum possible load to be taken. We have used as approximations the maximum observed load sizes (8 for maggots and 4 for mealworms). The predicted load sizes according to the Oriens-Pearson model and the observed average load sizes were not significantly different (Wilcoxon signed-rank test), while the load sizes predicted by the energy efficiency model were systematically larger or even unrealistically high (larger than the maximum observed loads in 8 of 15 cases), and differed significantly from the observed average values (Wilcoxon signed-rank test, $P < 0.01$).

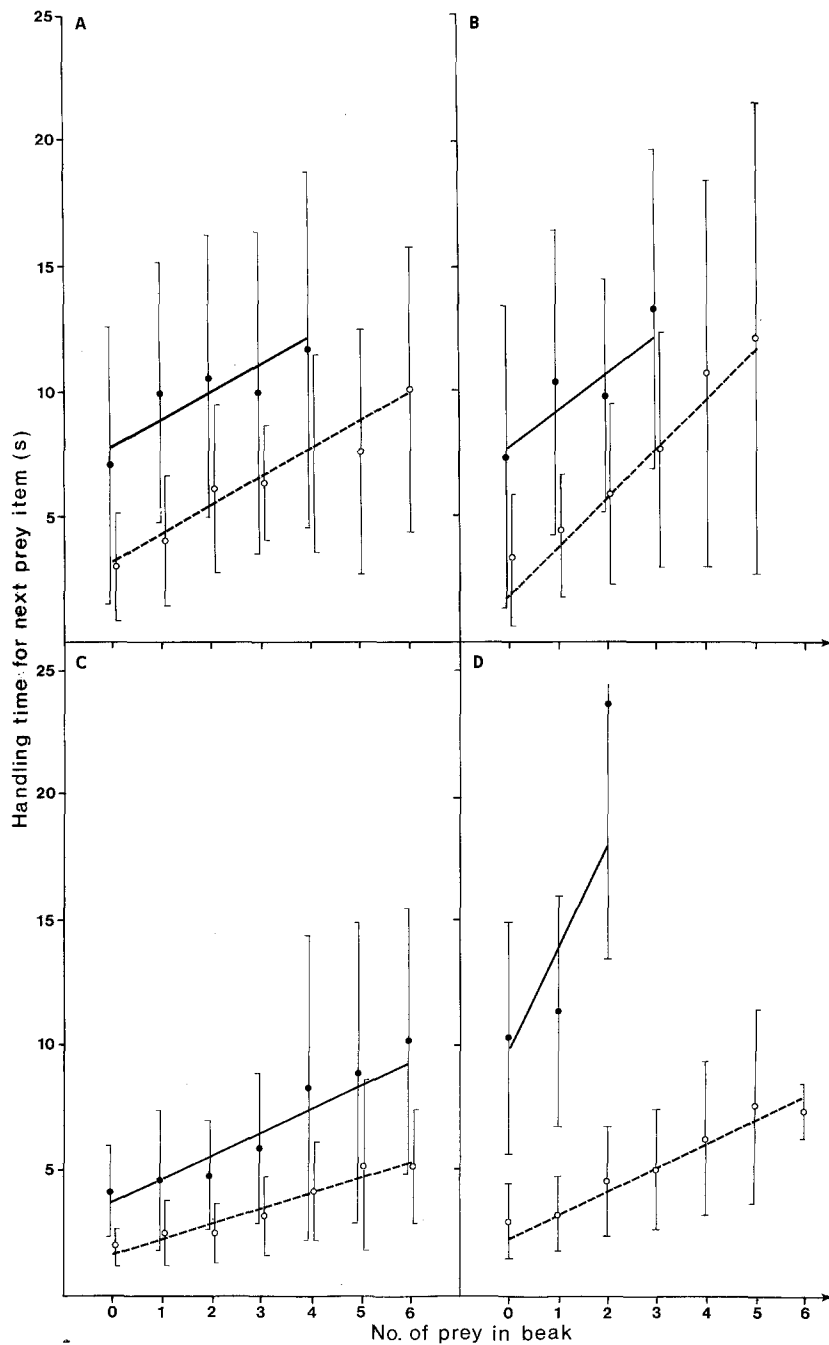


Fig. 3. Handling times ($\bar{x} \pm SD$) for maggots as a function of the number of prey held in the beak for male I (**A**), female I (**B**), male II (**C**) and male III (**D**), first period (black dots) and second period (white dots). Linear regression equations for first period (solid line) and second period (broken line) and correlation coefficients are:

| | |
|-------------------|--|
| A Period I | $Y = 6.79 + 1.08X,$ $r = 0.22, P < 0.001$ |
| Period II | $Y = 2.21 + 1.11X,$ $r = 0.47, P < 0.001$ |
| B Period I | $Y = 6.30 + 1.48X,$ $r = 0.68, P < 0.001$ |
| Period II | $Y = 1.91X,$ $r = 0.68, P < 0.001$ |
| C Period I | $Y = 2.85 + 0.93X,$ $r = 0.42, P < 0.001$ |
| Period II | $Y = 1.02 + 0.62X,$ $r = 0.56, P < 0.001$ |
| D Period I | $Y = 5.78 + 4.10X,$ $r = 0.47, P < 0.001$ |
| Period II | $Y = 1.29 + 0.96X,$ $r = 0.84, P < 0.001$ |

The average load size of maggots taken in high-density patches increased during the first 5–6 days of visiting the patches for all individuals, and then reached a plateau (Fig. 8). Female II started to load maggots 5 days later than her mate in relation to hatching date, and her average loads during the first days of loading were smaller than those of the male during the same days (Fig. 8). The individual trends in load sizes thus seem to be affected by the number of days in which the birds had been loading prey in the patches.

Discussion

The central-place foraging model of Orians and Pearson (1979) for multiple-prey loaders was based on the existence of the so-called loading effect (Kramer and Nowell 1980). Wheatears can pick up prey items while having those previously collected ones in the beak, and they do not need to drop these before picking up the new ones. However, such behaviour has a cost. The number of prey already taken has an effect on the collecting rates

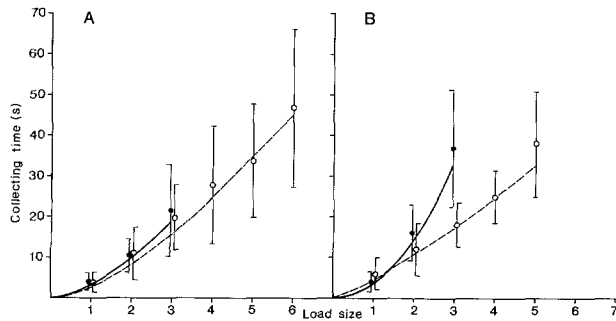


Fig. 4. Loading curves for two prey types, maggots (*broken lines*) and mealworms (*solid lines*), in high-prey density patches, for male I (**A**) and female I (**B**). Means and standard deviations of collecting times for all prey taken according to their ordinal number in prey capture sequences are shown for maggots (*white dots*) and mealworms (*black dots*). Values of n are number of round-trips observed. Loading functions are: **A** Maggots, $y = 3.13x^{1.47}$, $n = 19$; Mealworms, $y = 3.47x^{1.57}$, $n = 27$. **B** Maggots, $y = 4.87x^{1.19}$, $n = 14$; Mealworms, $y = 3.43x^{2.09}$, $n = 21$

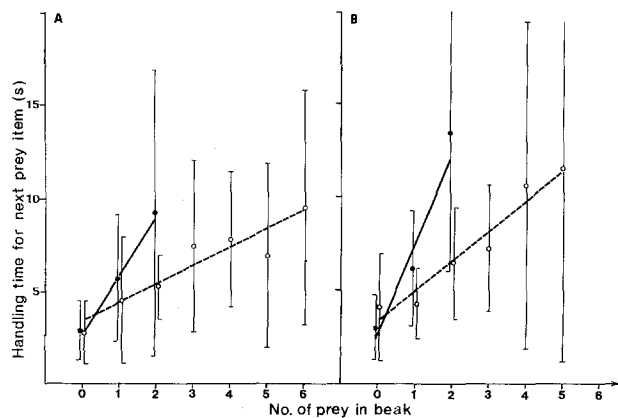


Fig. 5. Handling times ($\bar{x} \pm SD$) for maggots (*white dots*) and mealworms (*black dots*) as a function of the number of prey held in the beak in high prey density patches for male I (**A**) and female I (**B**). Linear regression equations (maggots-*broken line*, mealworms-*solid line*) and correlation coefficients are: **A** Maggots $Y = 1.01 + 2.37X$, $r = 0.45$, $P < 0.001$; Mealworms $Y = -0.25 + 3.08X$, $r = 0.50$, $P < 0.001$. **B** Maggots $Y = 1.70 + 1.62X$, $r = 0.45$, $P < 0.001$; Mealworms $Y = -2.13 + 4.76X$, $r = 0.70$, $P < 0.001$

of these birds (Fig. 2), as shown by the positively accelerating loading functions (Figs. 1, 4 and 6) and by the significant increase in handling times (Figs. 3 and 5). There was an increase in loading efficiency due to training in our experimental patches (Figs. 1 and 3). Familiarity with a certain prey species may affect loading efficiency and therefore the optimal load sizes for that prey type for a given travel time. This would imply that loading efficiency has an effect on prey profitability. The difference in loading effects for the two prey types (Figs. 4 and 5) also emphasizes the im-

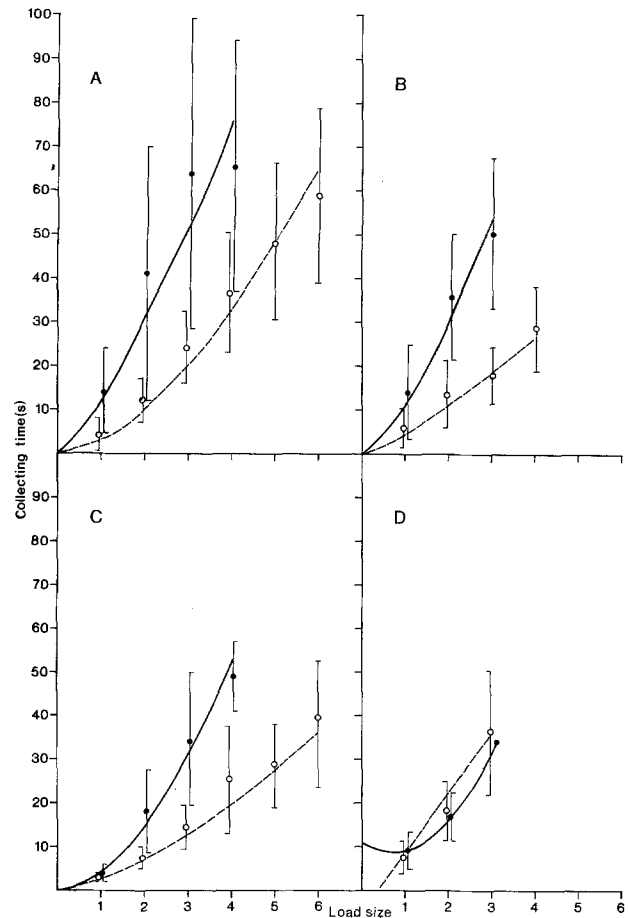


Fig. 6. Loading curves for low-prey density (*solid line*) and high-prey density (*broken line*) patches of maggots for male I (**A**), female I (**B**), male II (**C**) and female II (**D**). Means and standard deviations of collecting times for all prey taken according to their ordinal number in prey capture sequences are shown for low- (*black dots*) and high-prey densities (*white dots*). Values of n are number of round-trips observed. Loading functions are: **A** High-prey density, $y = 3.12x^{1.71}$, $n = 9$; Low-prey density, $y = 11.91x^{1.34}$, $n = 35$. **B** High-prey density, $y = 4.70x^{1.27}$, $n = 9$; Low-prey density, $y = 11.39x^{1.42}$, $n = 20$. **C** High-prey density, $y = 2.72x^{1.44}$, $n = 20$; Low-prey density, $y = 4.10x^{1.84}$, $n = 46$. **D** High-prey density, $y = -5.01 + 13.36x$, $n = 7$; Low-prey density, $y = 10.92 - 6.35x + 4.71x^2$, $n = 14$

portance of loading rates in determining load sizes for different prey. For loads of mixed prey types, which are very common in natural situations, different loading functions would make it very difficult to predict an optimal load.

It could be argued that the high-prey densities in these experiments are seldom present in natural situations. As Kramer and Nowell (1980) pointed out, the relative influence of the observed loading effect would decrease as food density decreased, since the handling component would then become a smaller proportion of total collecting time. The

Table 3. Average load sizes (\pm SD) of maggots taken and average patch times (\pm SD) in seconds spent in patches of high- and low-prey density by four individual wheatears. Results of two-way ANOVA tests: a) For load size with prey density as grouping factor: $F=61.11$, $P<0.001$. b) For load size with pair member as grouping factor: $F=20.44$, $P<0.001$. c) For patch time with prey density as grouping factor: $F=14.96$, $P<0.01$. d) For patch time with pair member as grouping factor: $F=25.78$, $P<0.001$

| | Load size | | Patch time | |
|-----------|-------------------------|-------------------------|---------------------------|---------------------------|
| | High-prey density | Low-prey density | High-prey density | Low-prey density |
| Male I | 5.7 \pm 1.7 (n=20) | 3.3 \pm 1.3 (n=57) | 86.9 \pm 36.7 (n=11) | 98.5 \pm 42.9 (n=43) |
| Female I | 4.4 \pm 1.4 (n=18) | 2.8 \pm 1.1 (n=29) | 57.8 \pm 20.0 (n=13) | 76.7 \pm 26.5 (n=22) |
| Male II | 5.2 \pm 1.3 (n=17) | 2.5 \pm 1.0 (n=40) | 38.1 \pm 27.3 (n=36) | 58.4 \pm 20.7 (n=40) |
| Female II | 3.0 \pm 1.4 (n=16) | 1.7 \pm 0.7 (n=11) | 37.5 \pm 11.0 (n=9) | 52.1 \pm 29.1 (n=10) |

Table 4. Average active search times \pm SD (s) for the first, second and third collected prey in patches of low-prey density by three individual wheatears. Only search times after which a prey was taken were considered. Results of two-way ANOVA tests: a) With no. of prey items as grouping factor: $F=13.63$, $P<0.001$. b) With individual as grouping factor: $F=6.08$, $P<0.01$

| | First prey | Second prey | Third prey |
|----------|-------------------------|-------------------------|---------------------------|
| Male I | 3.2 \pm 2.7 (n=30) | 7.1 \pm 7.1 (n=36) | 4.2 \pm 2.7 (n=32) |
| Female I | 3.3 \pm 2.3 (n=21) | 5.3 \pm 5.4 (n=18) | 7.5 \pm 7.9 (n=13) |
| Male II | 4.9 \pm 3.7 (n=72) | 7.6 \pm 6.2 (n=23) | 10.2 \pm 10.5 (n=17) |

loading curves would then approach linearity, increasing the advantage of maximal loads. In our low prey density patches, we tried to test if previously captured prey would interfere with searching efficiency, which would make the loading effect more pronounced for these patches and lead to smaller loads being taken. Searching in our patches included failed attempts to take the detected prey by pecking at the transparent sides of the cups and/or removing the moss layer. These activities took more time when the bird had more prey in the beak (Table 4). As a result of this increase in search time, loading functions in low-density patches rose more steeply, which led to the birds taking smaller loads and staying as long or longer in low-density than in high-density patches (Table 3), as predicted by the Orians-Pearson model.

Although some qualitative predictions from the Orians-Pearson model seem to be upheld in studies of different species (Kramer and Nowell 1980; Brooke 1981; Carlson and Moreno 1981; Tinbergen 1981; Giraldeau and Kramer, in press), it is also necessary to test the model quantitatively. Earlier studies have not derived proper loading functions (Tinbergen 1981), not clearly proved the existence of a loading effect (Killeen et al. 1981) or have disregarded individual patterns (Giraldeau and Kramer, in press). In the present case, our aim was to predict from the existence of positively accelerating loading functions the load sizes to be taken by individual birds in different situations.

There are several problems with quantitative tests of optimal foraging theory. Although the loading functions represent continuous processes, the optimal decision rules are discrete in the present case. The decision to leave the patch always occurred immediately after loading the n th prey

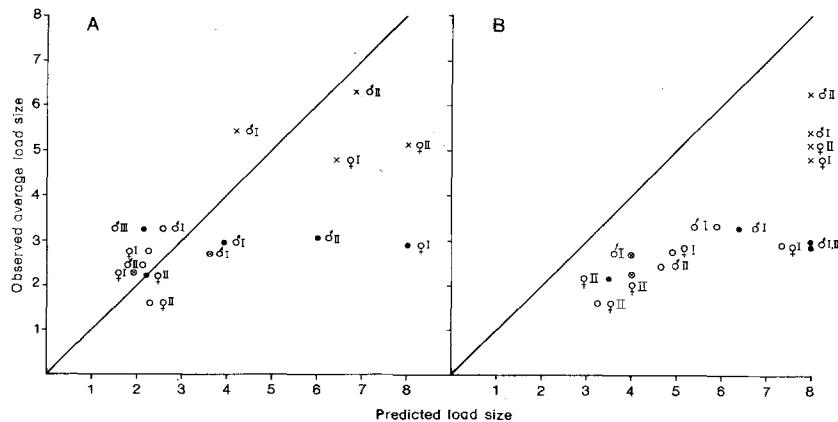


Fig. 7. The relationship between observed average load sizes and the predicted optimal load sizes according to the delivery rate model of Orians and Pearson (A) and to an energy efficiency model (B) for each individual and experimental setup. All predicted values greater than the maximum observed load sizes are equated to 8 for maggots and 4 for mealworms. ● – first period; × – second period; ○ – low-prey density; ⊙ – mealworms

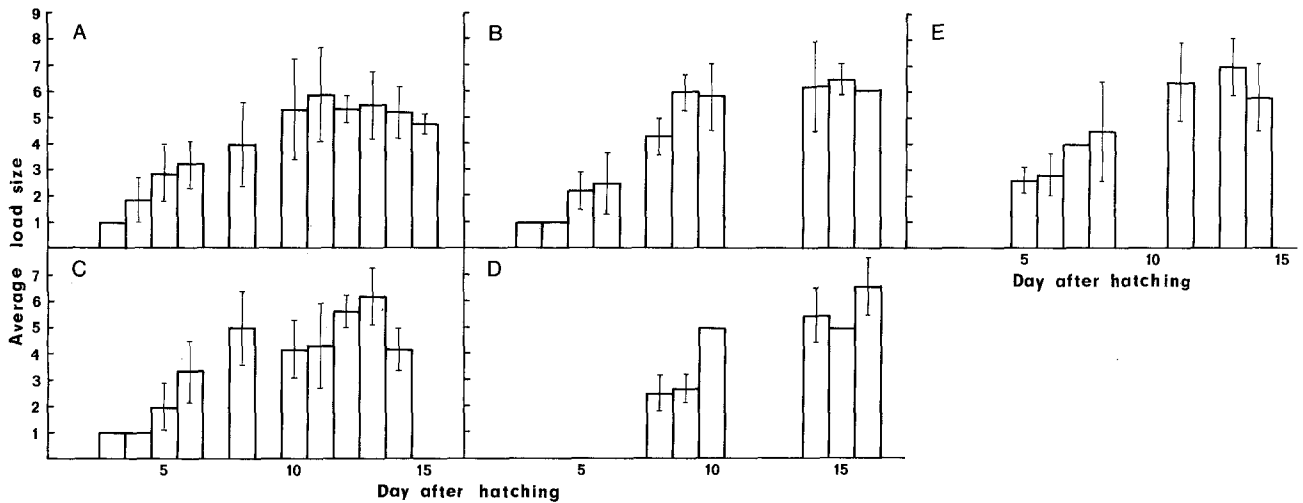


Fig. 8. Average load size for all days of the nestling period in which male I (A), female I (B), male II (C), female II (D) and male III (E) fed at high-density patches of maggots (vertical bars are standard deviations). The maximum observed load was 8

item. Thus, we should not expect complete concordance between the predicted and observed average load sizes in every case, as the estimated loading functions are only approximations to the actual loading processes. Another problem exists in terms of testing the predictions of optimal foraging models. The solutions to these models are calculated on the basis of estimates of parameters that are random variables. Hence there is a statistical error included in the solution and the predictions should be calculated as confidence intervals for the probability that the solution lies within this interval (Pyke 1981). Although the parameters of the loading function for each round trip are subjected to random variation, we have based our predictions of optimal load sizes on a single loading function without estimates of the associated error. Other studies have also calculated the optimal solutions without confidence intervals (Cowie 1977; Killeen et al. 1981; Tinbergen 1981; Giraldeau and Kramer, in press). The question arising at this point is how great should the differences be between the predictions derived from the model and the actual data in order to allow us to reject the hypothesis of the model.

In our case, although the fit between the values observed and predicted by the delivery rate model (Fig. 7a) is not perfect, the differences were not significant. However, if time in the nest is included in the total round-trip time (Kacelnik, personal communication), the results would be affected for the first period, as the parents usually stayed in the nest for more than 10 s for each visit when the nestlings were small. This would greatly in-

crease the predicted load sizes for that period. The predictions for the second period would not be affected, as the nest visits are very short at that stage (~2–4 s). However, it is doubtful if nest-time can be considered as part of a foraging round-trip, as the parents normally use that time for other functions also, e.g. brooding, cleaning the nest, waiting for and removing faecal sacs, etc.

It is also clear from our observations that the observed average load sizes are more in accord with those predicted by the original delivery rate model (Orians and Pearson 1979) than with those generated by the energy efficiency model (Fig. 7). This result contradicts observations of other studies (Cowie 1977; Kacelnik, personal communication). It would imply that the parent birds were sacrificing energetic efficiency in favour of a greater delivery rate. For birds feeding nestlings, it may be more important to maximize the growth rate of the young than to maintain a well-balanced energy budget.

Acknowledgements. We thank M. Andersson, P.R. Grant, D.H. Morse and S. Ulfstrand for reviewing a draft of this paper and R.V. Alatalo and T. Fagerström for their helpful suggestions. A. Kacelnik discussed our MS and his unpublished data with us and suggested new aspects. L.-A. Giraldeau kindly sent us an unpublished MS on a related subject.

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