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Quantifying food limitation of arthropod predators in the field

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Abstract A method for quantifying food limitation of arthropod predators in the field is presented and applied to species of ground beetles (Carabidae) and sheet-web spiders (Linyphiidae) from a cereal field. Food limitation is expressed quantitatively as accumulated hunger (= starvation) by transforming 24-h food consumption at 20°C of animals newly collected in the field into days of starvation at 20°C. This is done by means of a reference curve relating 24-h food intake at 20°C to starvation periods (days) at 20°C. Such a reference curve was obtained for the carabid beetle *Agonum dorsale* in the laboratory. For other species the reference curve was modified with species-specific data. The procedure makes it possible to compare the feeding conditions of different species populations that are part of the same community. Hunger levels in the field for females of *A. dorsale* were equivalent to *c.* 15 days of starvation in early spring, *c.* 5 days in June, increasing to *c.* 10 days in late summer. Two ground beetles occurring during summer also showed increasing hunger levels from June to July, probably the result of a dry summer. Two spider species experienced a hunger level in the range of 4–8 days of starvation.

Key words Ground beetles · Linyphiid spiders · Food consumption · Starvation

Introduction

Food limitation is often a decisive ecological factor for populations and individual animals at some stage of their life-cycle (White 1978); occasionally it may be a chronic state of affairs with which animals should be adapted to cope. Spiders are generally believed to have evolved under constant pressure of food shortage and show many adaptations to this in physiological (Anderson 1974) and ecological details (review in Wise 1993). Other polyphagous predators sharing the same general food resources, e.g. carabids, are frequently food-limited (Lenski 1984; Pearson and Knisley 1985; Juliano 1986; Van Dijk 1986) though this aspect of their biology is less well studied.

Most demonstrations of food limitation of predatory arthropods in the field infer it from comparisons of growth rate (Griffiths 1980; Pearson and Knisley 1985; Miyashita 1968; Juliano 1986), survival (Wise 1975) or fecundity under natural and supplemented food levels (Wise 1975, 1979; Pearson and Knisley 1985; Sota 1985; Van Dijk 1994). Here we introduce a more direct method of assessing the degree of food limitation experienced by a predator at a particular stage of its life cycle. In the procedure proposed here food limitation is indicated by quantifying hunger levels in the field at regular intervals through the season, thus describing both the levels of hunger and their seasonal occurrence. Since food availability may change drastically over a season, depending on abiotic as well as biotic factors, some phases of the animal's life cycle may be more affected than others; thus, it would be useful to be able to track closely such changes in the degree of food limitation. We apply the method to species of ground beetles (Carabidae) and sheet-web spiders (Linyphiidae) from a Danish cereal field and follow fluctuations in hunger levels during spring and summer.

Materials and methods

General procedure

The relationship between starvation time and food consumption was found and used to indicate hunger levels in the field from measurements of consumption rates in newly collected field predators. The following three steps were involved:

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1. Establish a reference curve that describes the relationship between 24-h food consumption (C) and starvation time in days (D) at 20°C.
2. Measure 24-h food consumption (C_{FIELD}) of newly collected field animals under the experimental conditions that were used for obtaining the reference curve.
3. Infer the hunger level of field animals (D_{FIELD}) expressed in days of starvation at 20°C by combining steps 1 and 2.

The relationship between C and D (step 1) is non-linear (Fig. 1), but can be linearized by appropriate transformations:

$$C^{Z_1} = a + bD^{Z_2} \qquad (1)$$

where C is 24-h food consumption (mg dry weight of food/mg live weight predator) at 20°C; D is number of days of starvation at 20°C; a (intercept) and b (slope) are constants; z_1 and z_2 are the exponents of the power transformations used to linearize the relationship; a is the minimum 24-h consumption needed to maintain satiation of previously satiated animals.

In order to perform step 3, Eq. 1 is solved for D and data from step 2 are inserted:

$$(D_{\mathrm{FIELD}})^{Z_2} = \frac{(C_{\mathrm{FIELD}})^{Z_1} - a}{b} \qquad (2)$$

$(C_{\mathrm{FIELD}})^{Z_1}$ was calculated as the average of transformed 24-h field consumption measurements of a sample, and then converted to $(D_{\mathrm{FIELD}})^{Z_2}$ by Eq. 2.

The $(1 - \alpha)$ confidence limits of the estimated field hunger levels were calculated from Hald (1960, p. 551):

$$(D_{\mathrm{FIELD}})^{z_2} \pm t_{1-\alpha/2^{(n_r-2)}} \frac{s}{b} \sqrt{\frac{1}{n_s} + \frac{1}{n_r} + \frac{[(D_{\mathrm{FIELD}})^{z_2} - \bar{x}]^2}{\mathrm{SSD}_x}} \qquad (3)$$

where $t_{1-\alpha/2^{(n_r-2)}}$ is the $(1 - \alpha/2)$-fractile of the t-distribution with $(n_r - 2)$ degrees of freedom; $s = \sqrt{s^2}$ where s^2 is the mean square deviation around the regression line of C^{z_1} of the reference data; n_s is the sample size of the field collected predators and n_r is the sample size of the reference data. Finally $\bar{x}$ and SSD_x are the mean and the sum of squares of deviation of the transformed number of days of starvation of the reference data. $D_{\mathrm{FIELD}} \pm 95\%$ confidence limits is found by inverse transformation of $(D_{\mathrm{FIELD}})^{Z_2} \pm 95\%$ c.l., which results in asymmetric confidence limits.

Reference curves

A complete reference curve (Eq. 1) based on five reference points was obtained for the carabid beetle *Agonum dorsale* (Pont.). The linear relationship of the reference data obtained for *A. dorsale* (Eq. 1) was also used for other species, except that specific values of a and b were obtained from partial reference curves based on only two reference points (see below), while maintaining the z_1 and z_2 values obtained for *A. dorsale*.

Females of *A. dorsale* were collected at the beginning of their reproductive season from early spring aggregations beneath stones in April 1995 at a locality near Århus, Denmark. They were fed freshly freeze-killed fruit flies *Drosophila melanogaster* (Meig.) ad lib over several days to be certain that they had reached satiation. Apparently carabids and spiders have a high preference for fruit flies and are able to reach satiation on this prey (Bilde and Toft 1994; Toft 1995). Separate series of animals were then starved for 0, 3, 7, 14 and 21 days, respectively, with 14–17 females in each series. After these starvation periods, 24-h food consumption was determined (see below). Different animals were used for all series except that the satiated group (0 days starvation) was reused for the 3-day starvation treatment.

The reference data were transformed (consumption/24 h raised to the power z_1) in order to obtain homogeneity of group variances (Bartlett's test). To find the best transformation of C, several values of z_1 were tested (Bartlet's test) and the one giving the largest homogeneity of group variances was selected. Using the selected z_1, several values of z_2 for transformation of starvation time, D, were tested in linear regressions, and the one giving the highest r^2 selected. Linearization of the reference curve was required for calculating confidence limits (Eq. 3).

Field hunger levels

Three carabid beetles (*A. dorsale*, *Calathus fuscipes* (Goeze) and *Pterostichus melanarius* (Ill.)) and two linyphiid spiders (*Erigone atra* (Bl.) and *Oedothorax apicatus* (Bl.)) were included in the analysis of hunger levels in the field. For each individual, 24-h field consumption measurement (C_{FIELD}) was initiated immediately after arrival at the laboratory. Additional data for the calculation of species-specific constants a and b were then obtained in the following way. The predators were fed to satiation with fruit flies ad lib for 1–2 days, after which 24-h food consumption was determined (C_{SAT}). Then they were starved for 7 days, after which 24-h feeding rates were determined once more ($C_{7-\mathrm{D}}$). The constant a is the species-specific 24-h satiation consumption needed to maintain satiation $(C_{\mathrm{SAT}})^{Z_1}$; b was calculated as: $[(C_{7-\mathrm{D}})^{Z_1} - (C_{\mathrm{SAT}})^{Z_1}]/7^{Z_2}$, using the values for z_1 and z_2 obtained from the reference curve for *A. dorsale* (Eq. 1). Equation 2 for calculation of field hunger levels was then corrected for each species analysed by the use of the species-specific constants. For *A. dorsale* two reference curves were obtained with the constants a and b calculated from the two separate data sets. Both methods were used in the calculation of field hunger levels for this species.

Employing this procedure we assume that the transformations estimated from the reference curve for *A. dorsale* apply to other carabid species as well. For the spiders, we tested the transformations on similar data sets from two other spider species. Consumption of fruit flies determined in the wolf spider *Pardosa prativaga* (L.K.) after 0, 3, 8 and 14 days of starvation (Toft 1995); and in the wolf spider *Schizocosa* sp. after 0, 7, 11 and 19 days of starvation (S. Toft and D.H. Wise, unpublished work). In both cases linear relationships were obtained.

Field sampling

Predators used for the field starvation measurements were collected from a winter wheat field at Kalø near Århus, Denmark, from May to August 1994. Most were collected below pieces (25 × 12.5 cm) of wooden planks laid out in the field to serve as hiding places for the animals during inactive periods. For carabids both sexes were sampled, while for spiders only females were collected.

Laboratory procedure

Predators collected for determination of field hunger levels were transported to the laboratory in a cooled bag. Within 2–3 h of capture they were weighed and the 24-h food consumption measurement was initiated for determination of C_{FIELD}. Following this, C_{SAT} and $C_{7-\mathrm{D}}$ were determined.

Feeding procedures and experimental conditions were the same for obtaining reference data and determining field hunger levels with a constant temperature of 20°C and a 16 L:8 D photoperiod. Spiders were kept in glass tubes with a moistened 1–2 cm pad of plaster-of-Paris with charcoal; beetles were placed in plastic petri dishes with a piece of moist cotton wool.

Spiders were offered live flies in numbers from 10 to 30, depending on size. Beetles were offered a weighed (wet weight) sample of freeze-killed fruit flies. On all feeding dates a counted and/or weighed sample of fruit flies was dried in a vacuum oven at 60°C for at least 2 days and then weighed in order to convert numbers or fresh weights of fruit flies offered to dry weights (dw). At the end of the experiment food remains were collected and their dry weight obtained as above. Food consumption in mg dw was then determined. For all species the weight-specific feeding rate was calculated in order to account for differences in food consumption caused by size differences.

Results

Reference curve

Feeding rate in *A. dorsale* increased at a decreasing rate as a function of starvation time (Fig. 1). The highest test probability for homogeneity of group variance was obtained with $z_1 = 0.60$ (Bartlett's test, $P = 0.152$). The best linear fit was obtained when $z_2 = 0.65$ (regression analysis, $r^2 = 0.654$). Thus, Eq. 1 becomes:

$$D^{0.65} = \frac{(C^{0.6} - 0.353)}{0.045} \tag{4}$$

The test probability of Bartlett's test and r^2 of the regression analysis were not very sensitive to small variations (± 0.1) in the transformations.

Field hunger levels were calculated with varying values of z_1 and z_2 in order to test the sensitivity of the linearized model to the accuracy of the power transformations. Deviations of magnitude ± 0.05 of z_1 and z_2 changed the results (field hunger levels in days of starvation) by ±2–3 days. These values are within the 95% confidence limits of the means estimated using Eq. 4.

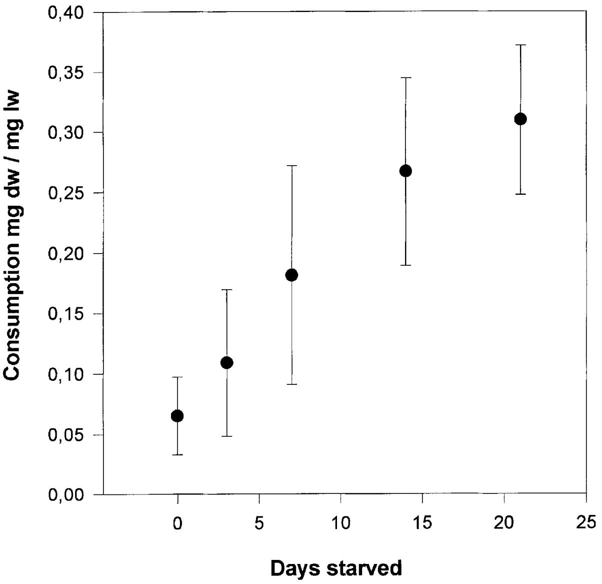

Fig. 1 Relationship between weight-specific food consumption (mg dry weight/mg animal) in *Agonum dorsale* (females) and starvation time (days); *error bars* show SD

Differences between sexes

There was no difference in consumption between females and males in any of the carabid species (ANOVA, $P > 0.05$ in all cases). Therefore sexes have been pooled in the analyses of species-specific constants *a* and *b*.

Field hunger levels

Agonum dorsale

Field hunger levels estimated with constants from the reference curve (Fig. 2A) and from $C_{SAT} - C_{7-D}$ data (Fig. 2B) show similar patterns. In Fig. 2B high starvation levels appear slightly higher and low levels slightly lower than in (Fig. 2A). According to both methods females reached severe hunger levels in May (10–20 days of starvation), whereas hunger levels for males were in the range of 5–10 days of starvation. The difference between the sexes is surprising in view of the fact that we found no sex differences in weight-specific food consumption of the same beetles in the C_{SAT} and C_{7-D} measurements. For both sexes starvation levels decreased to *c.* 5 days at the end of June, and then increased again to approximately 10 days at the beginning of August.

Oedothorax apicatus

With a starvation level of *c.* 7 days in May (Fig. 3) the spider suffered less hunger in spring than *A. dorsale*. The hunger level decreased to 3–4 days of starvation in June and then increased to 7–9 days of starvation in early July and August.

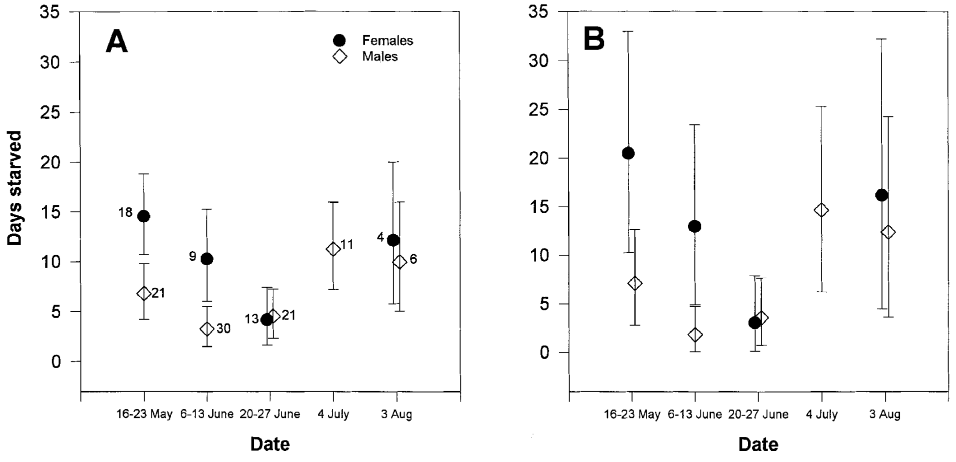

Fig. 2A, B Hunger levels in the field in days of starvation for *A. dorsale* (males and females). **A** Constants *a* and *b* calculated from complete reference data (0, 3, 7, 14, 21 days of starvation), **B** constants *a* and *b* calculated from partial reference data C_{SAT} and C_{7-D}. *Error bars* show 95% confidence limits; *numbers* are sample sizes

Calathus fuscipes

Starvation levels in *C. fuscipes* (Table 1) increased from mid June to the beginning of July and then decreased through July. The picture was the same for both sexes, but hunger levels for females were generally higher than for males.

Pterostichus melanarius

There is only a small data set for *P. melanarius* (Table 1), but the picture is the same as for the two other carabid species, with an increase in hunger level from the middle of June to early July. Apparently there was no difference between females and males.

Erigone atra

Throughout June hunger levels were constantly at *c.* 7 days of starvation (Table 1). The relatively large 95% confidence limits for the species reflect the relatively small sample sizes.

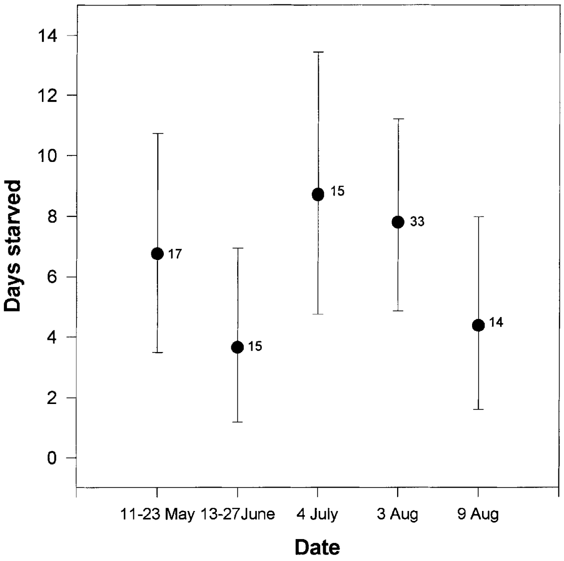

Fig. 3 Hunger levels in the field in days of starvation for *Oedothorax apicatus* (females). *Error bars* are 95% confidence limits, *numbers* are sample sizes

Table 1 Hunger levels in the field: mean days starved at 20°C ± (95% confidence limits) for species of arthropod predators (females and males) over varying periods [Date (*n* females, *n* males)]

	Females	Males
Calathus fuscipes		
13 June (7, 13)	9.15 (1.94–19.51)	6.26 (1.49–12.98)
4 July (8, 9)	23.1 (8.47–42.19)	12.83 (4.11–24.52)
3 August (9, 13)	7.71 (1.69–16.31)	0.11 (0–3.46)
Pterostichus melanarius		
3 June (6, 6)	6.72 (0.98–15.41)	6.67 (0.96–15.34)
4 July (4, 4)	16.58 (4.75–32.75)	16.57 (4.27–33.68)
Erigone atra		
3 June (7)	7.43 (2.18–14.58)	
13 June (8)	7.63 (2.38–14.93)	
27 June (7)	6.34 (1.69–12.79)	

Discussion

Field hunger levels

Our results reveal substantial hunger levels in the field and drastic seasonal changes, at least for *A. dorsale*. The study reflects the situation in one field under the physical and biological conditions of one particular year. Because species-specific feeding rates are translated into the common currency of days of starvation at 20°C, it is possible to compare hunger levels between species. All predators tested were food-limited to some degree all the time, June being the period of least food limitation. Hunger levels increased again in July, probably due to a change in weather to hot and dry conditions that could have reduced the number of prey available. How food availability influences the predator populations overall, i.e. in terms of reproductive success, may depend on which stages of the life cycle experience food shortage. *A. dorsale* and *O. apicatus* both reproduce in early spring, so it can be hypothesized that their egg production is limited by food availability. The fact that they produced eggs within 1 or 2 days of arrival to the laboratory demonstrates that they are adapted to reproduce even under severe food shortage.

We expected females of *A. dorsale* in spring to have a larger weight-specific food demand than males, due to egg production, and while this tendency was found in the field hunger measurements it could not be shown when hunger level was experimentally controlled in the food consumption measurements (C_{SAT} and $C_{7\text{–}\mathrm{D}}$). The lower hunger levels of males in the field then need an explanation. Females are larger than males, which means that their food demand per individual is larger than that of males. Furthermore they have to spend time finding suitable oviposition places and laying their eggs, and thus have less time available for foraging. Males search for females but may be able to combine this with searching for food; overall, this could lead to lower hunger levels in males than in females.

Methodology

The hunger levels found in the field in the present study obviously arose under very different temperature conditions at various times of the season. However, they were all measured at 20°C and expressed as days of starvation at 20°C. To obtain a certain hunger level measured at this temperature requires a longer starvation period at the early spring temperatures than in the warm season. The question of whether the temperatures experienced by the predators in the field prior to the feeding experiments affect the amounts eaten during 24-h food consumption at 20°C can be raised. O.F. Sørensen (unpublished work) kept the carabid *Bembidion lampros* (Hbst) at 5°C and 20°C respectively prior to feeding experiments at 20°C and found no difference in 24-h food consumption. Since the animals in spring are normally subjected to diurnal temperature fluctuations exceeding these values, we believe that field animals are not acclimated to any particular temperature; for this reason we expect them to be able to adapt immediately to any temperature within the normal range.

Ideally a complete reference curve like the one obtained for *A. dorsale* should be obtained for each species investigated. We would expect, though, that the shape of the reference curve (Fig. 1), where food consumption increases at a negatively accelerating rate as a function of hunger, will apply to all arthropod species. Also different stages of life history should be taken into consideration, as the relationship between food consumption and hunger could vary between growth stages. We chose to work with adult animals exclusively in this study, thus reducing the variation in size.

In *A. dorsale* we estimated hunger levels in the field with the constants *a* and *b* calculated from two separate data sets. Similar field hunger levels were obtained by the two methods (Fig. 2). This indicates that the calculation of *a* and *b* based on a reduced data set (C_{SAT} and $C_{7-\mathrm{D}}$) gives reasonable estimates of these constants.

The method presented here quantifies food limitation in the field directly. It is sensitive in that changes in the habitat influencing food availability can be detected immediately and across populations and species. Procedures of estimating food availability indirectly, e.g. by measuring egg production rates (Wise 1979; Van Dijk 1994) reflect the food situation of the predator over a longer period. The use of body condition indices (Baker 1989; Juliano 1986) to infer relative food availability in some cases has proven to be sensitive to variation in body size, which may have a major influence on interpretation of the results (see discussion in Jakob et al. 1996). Jakob et al. 1996 found the residual index to be effective in separating effects of condition from those of body size, but they point out that residuals are not comparable across populations. Vollrath (1988) presented a method for calculating body reserves and thus the food intake of spiders in the field. A calibration curve providing the relationship between accumulated reserves and spider growth ratio was obtained in the laboratory; from this curve body reserves of field animals could be inferred from field data on growth rate and growth ratio (Vollrath 1988). The method gives information about feeding rates within instars, but is restricted to use for juveniles, as growth parameters are measured between moults.

The method we propose is more laborious than the use of simple body-condition indices (Jakob et al. 1996). However, because we directly measure hunger levels in the field our results are more easily interpretable. Further, it can be accomodated to growing and reproducing life cycle phases equally well. By monitoring hunger levels regularly over the life cycle, a precise description of the feeding conditions of a population can be obtained. It is highly likely that a certain degree of food limitation has different effects on individual fitness depending on which life cycle stage is affected. Such relationships can be analysed by combining measurements of fitness effects of food limitation with the measure of food limitation as accumulated hunger. The procedure presented here can be refined and adapted to special situations, but in principle we believe it will apply to any arthropod predator in any habitat type. Because individual hunger is transformed into a common currency that is independent of individual or species characteristics, the method can be applied to all possible intra- and interspecific comparisons, within and between habitats and along seasonal and yearly time axes.

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