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Estimating Fitness: A Comparison of Body Condition Indices

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## Estimating fitness: a comparison of body condition indices

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Behavioral ecologists might often benefit by the ability to directly measure an animal's body condition as an estimate of foraging success, and ultimately fitness. Here we compare the reliability and effectiveness of three indices of body condition that have been heavily used in the morphometrics literature. We examined the ratio index (body mass/body size), the slope-adjusted ratio index (based on regression slopes generated from a reference population), and the residual index (the residuals of a regression of body mass on body size). We present the results of tests performed in the field and laboratory on two ecologically and evolutionarily divergent spider species: the vagrant wolf spider *Pardosa milvina* (Araneae, Lycosidae), and the colonial orb-weaver *Metepeira incrassata* (Araneae, Araneidae). The ratio index correlated with body size, which weakened the strength of conclusions that could be drawn. The slope-adjusted ratio index requires an independent and large data set with which to generate the expected values, and was likewise sensitive to body size. The residual index, with appropriate transformations to achieve homoscedasticity, was the most reliable index because it did not vary with body size, and we recommend its general use in behavioral studies that require a condition estimate.

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An animal's physiological state is potentially related to its evolutionary fitness. Its health can be an indicator of past foraging success, fighting ability, and ability to cope with environmental pressures; any of these may ultimately impact reproductive success. Assessments of physiological state include tests of stamina, such as forced exercise (e.g., Thorpe et al. 1995), direct measurement of fat content (e.g., Marden and Rollins 1994), etc., but these can be difficult to do in the field, overly time-consuming, very intrusive, or even fatal to the subject. Similarly, an animal's lifetime reproductive success is often difficult or impossible to measure. Instead, ecologists have measured body condition, an estimate of nutritional state (i.e., relative "fatness"), to provide a snapshot of an animal's physiological state: one simply takes linear measures or weights of the subjects and constructs an index with one of a variety

of techniques. Our purposes here are (1) to draw the attention of behavioral ecologists to three different methods of estimating condition, and (2) to provide comparisons of each method with data from experimental studies to suggest which index is best.

Methods of calculating condition share the common goal of controlling for absolute body size when comparing body mass or other measures of nutritional state across individuals. Many terms have been used to describe body condition: condition (Le Cren 1951, Bolger and Connolly 1988, Baker 1989), condition index (Hepp et al. 1986, Moeller 1987, van Berkum et al. 1989, Matlack and Evans 1992, Renouf et al. 1993, Sweitzer and Berger 1993), condition factor (Juliano 1986), physiological condition index (Lucas and Beninger 1985), and the weight-length coefficient or the ponderal index (Thompson 1942). We will use the term

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“condition index” to encompass the range of indices in the literature. Here we have selected three commonly used indices for comparison.

The simplest index we have identified, hereafter called a *ratio index*, is generally calculated as body mass divided by a linear measure of body size. In a variation of this method, the linear measure is raised to a power, generally a power of three; this assumes that mass and linear dimensions increase isometrically (Cone 1989). This method was originally developed for and has been extensively used by the fisheries industry (reviewed by Le Cren 1951). Behavioral researchers have also used the ratio index. For example, Greenstreet (1992) studied changes in condition over time in salmon migrating down a release ladder. Tonn et al. (1989) found that the ratio index of crucian carp was higher in the presence of a predator. The repeatability of individual differences in locomotor performance and a ratio index in lizards was studied by van Berkum et al. (1989). Moeller (1987) used body weight divided by (wing length)<sup>3</sup> in a study of plumage badge size in the house sparrow. In a study of the daily energy expenditure of iguanas, van Marken Lichtenbelt et al. (1993) used a ratio index. Evans and McMahon (1987) used a ratio index of (mass)<sup>2</sup>/culmen length to study the relationship between food deprivation and brood reduction in pelicans. Anderson (1974) divided abdomen width by carapace width to measure condition in spiders.

In the *slope-adjusted ratio index*, a “standard” population is used to generate the slope of the regression of ln(body mass) against ln(length of a body part). This slope is then used to generate the index for each organism (*i*) in the test population, with the formula

$$\text{slope-adjusted ratio index} = \frac{\text{mass}_i}{(\text{length}_i)^{\text{slope}}} \quad (1)$$

This differs from the ratio index only in that the slope of the line is generated from independent data, instead of being assumed on the basis of general relationships in body shape (Cone 1989). Nicoletto (1993) used the slope-adjusted ratio index to address the question of whether ornaments of male guppies are condition-dependent. Külling and Milinski (1992) found a relationship between the slope-adjusted ratio index and the tendency of stickleback fish to inspect a predator. The slope-adjusted ratio index has been used in insect studies, including those of food limitation in bombardier beetles (Juliano 1986) and competition in odonate larvae (Pierce et al. 1985, Baker 1989). Watson (1990) used a variation of the slope-adjusted ratio index, in which he generated expected weights for spiders of a particular carapace width, in a study of male-male competition over mates by sierra dome spiders.

The *residual index* is fundamentally different than either of the ratio indices. Here, body mass is regressed on body size after the data are appropriately trans-

formed to meet the assumptions of regression (generally ln transformations are successful). The residual distances of individual points from this regression line then serve as the estimators of condition. This method, suggested by Gould (1975), was developed for comparative biologists who sought to control for body size when comparing the size of morphological structures across species and higher taxa (Harvey and Pagel 1991). In behavioral studies, Marden and Rollins (1994) tested whether aerial contests in damselflies were ended when fat stores were depleted. Fat content was estimated by chloroform extraction, then regressed on lean dry body mass to provide the residuals. Hamer and Furness (1993), in a study of aggression in brood defense of great skuas, used a residual index to estimate condition.

We measured body condition because we were interested in estimating the recent foraging success of spiders and needed a fast, non-invasive procedure. Body condition is likely to be linked to future fitness: in other spider species, feeding success correlates with growth rates (e.g., Jakob and Dingle 1990) and egg production (e.g., Morse 1988). We were motivated to compare the performance of different condition indices when we discovered that our choice of index dramatically influenced our results. In choosing which measurements to take, we took advantage of the fact that the unsclerotized abdomen of spiders readily expands and contracts with feeding and starvation. Arachnologists have calculated indices by dividing a measure of abdomen size by a measure of a heavily sclerotized body part that does not change in size with feeding (e.g., Anderson 1974, Watson 1990, Jakob 1991). In this paper, we compare the ratio index, the slope-adjusted ratio index, and the residual index for two empirical data sets from two spider species. These species differ in both body shape and natural history; one is a cursorial hunter and one is an orb weaver. We present results from both laboratory and field data.

## Methods and materials

### Case study 1: *Pardosa*

*Pardosa* wolf spiders (Lycosidae) are widespread and abundant hunting spiders in the eastern United States. We collected *P. milvina* Hentz from soybean fields as part of an ecological study of this species in a soybean agroecosystem under different tillage regimes. Research was conducted in the field and laboratory at Miami Univ. in Oxford, Butler County, Ohio, USA. We tested our three condition indices on two groups of spiders with two treatments within each group: those from the field (till vs no-till agricultural fields) and those from a laboratory rearing study (high vs low feeding level).

### Field studies

Fourteen juvenile and adult female spiders were collected from the till plots and 38 from the no-till plots. Spiders were hand-collected by searching 60 1.0-m<sup>2</sup> quadrats during daylight hours in September 1994. Additional spiders were collected in dry cup (live capture) pitfall traps along a drift fence. All spiders were brought back to the lab alive and immediately weighed and measured.

### Laboratory studies

A group of 22 early-instar *Pardosa* were collected in the vicinity of the study plots used above, brought into the lab, and individually reared in 35.6-ml plastic vials. A strip of brown paper toweling dampened with distilled water provided moisture and substratum. Vials were kept in an environmental chamber at 25°C and an L:D 12:12 cycle. Spiders were weighed, fed domestic crickets (*Acheta domestica*), and watered twice a week. Carapace width was measured when the spiders molted. Two feeding regimes were used: *high* – an amount of food equal to each spider's body mass twice a week; *low* – an amount of food equal to half of each spider's mass once a week. Thus, the low-fed group received food at one-quarter the rate of the high-fed group. The experiment was run for 8 weeks (3 November–22 December 1994).

### Estimation of body size

We chose carapace width as our estimator of body size because this appears to be the best estimator of body mass for spiders (Hagstrum 1971, Marshall and Gittleman 1994). Measurements were made using an ocular micrometer mounted on a dissecting microscope at 12× magnification. Spiders were weighed to the nearest 0.1 mg on an electronic balance.

### Calculation of indices and statistical analyses

The three measures of condition were calculated as follows: (1) The ratio index for field and laboratory spiders was calculated by dividing mass (mg) by carapace width (mm). The treatment groups (field: till vs no-till; laboratory: high vs low food) were compared using a *t*-test. (2) For the slope-adjusted ratio index, the slope of  $\ln(\text{body mass in mg})$  against  $\ln(\text{carapace width in mm})$  was calculated from field-collected spiders. This slope was then used to estimate the conditions of laboratory-reared spiders using eq. 1. We compared the indices of the high and low fed groups with a *t*-test. (3) We tested the residual index for both lab and field spiders. For each group, we regressed  $\ln(\text{body mass})$  on  $\ln(\text{carapace width})$ . The residuals for each treatment group (field: till vs no-till; laboratory: high vs low food) were compared with a *t*-test.

## Case study 2: *Metepeira*

*Metepeira incrassata* F. O. Pickard-Cambridge (Araneidae) is a communal-territorial spider. These spiders cooperate in building a semi-permanent communal frame web. Within the frame web each individual defends its own orb, which it ingests every evening and builds again in the morning. We were interested in estimating recent foraging success of field-caught spiders in order to determine how energy level affects a spider's choice of location in a colony, and to incorporate this information into a dynamic model, a technique well-suited to studies of behaviors that vary according to an animal's state (Mangel and Clark 1988, Clark 1991).

### General methods

Our study population was in Fortín de las Flores in Veracruz, Mexico. In August–October 1992 and 1993, we captured spiders from the field, took them to the laboratory, placed them in small vials, and treated them in one of three ways: starved for 8–9 d (with access to water), fed to capacity with houseflies (*Musca domestica*), or held overnight as a control (1993 only). Before and after treatment we used dial calipers to measure the length of the first tibia, carapace width, abdomen length, and abdomen width to the nearest 0.1 mm. For larger spiders we also measured abdomen depth, but it was not feasible to do this with small spiders. In 1992 we also measured mass (mg) with an electronic balance.

### Estimation of body size

It was difficult to measure carapace width accurately, so we chose length of the first tibia as an estimator of spider size. In addition, because we did not have a balance in the field in 1993, we needed to estimate mass from linear measures. *Metepeira* abdomens approximate an ellipse in shape, so we estimated abdomen volume from linear measurements. In cases where abdomen depth was known, we used the formula for the volume of an ellipse,  $4/3\pi lwd$ , where  $l$  = abdomen length/2,  $w$  = abdomen width/2, and  $d$  = abdomen depth/2. In 1992, abdomen volume was a good predictor of mass in a regression ( $r^2 = 0.94$ ,  $df = 1, 147$ ,  $P = 0.0001$ ). Volume predicted mass more accurately than did any one of the three linear abdominal measures.

### Calculation of indices and statistical analyses

We calculated the three condition indices with the post-treatment measurements from 1993. (1) For the ratio index, we divided abdomen volume by length of the first tibia. (2) For the slope-adjusted ratio index, we generated a regression of  $\ln(\text{abdomen volume in mm}^3)$  vs  $\ln(\text{tibia length in mm})$  from 1992 field-caught spiders; this provided a separate reference population. We then calculated the index for the 1993 post-treatment spiders based on this slope. We also calculated the slope

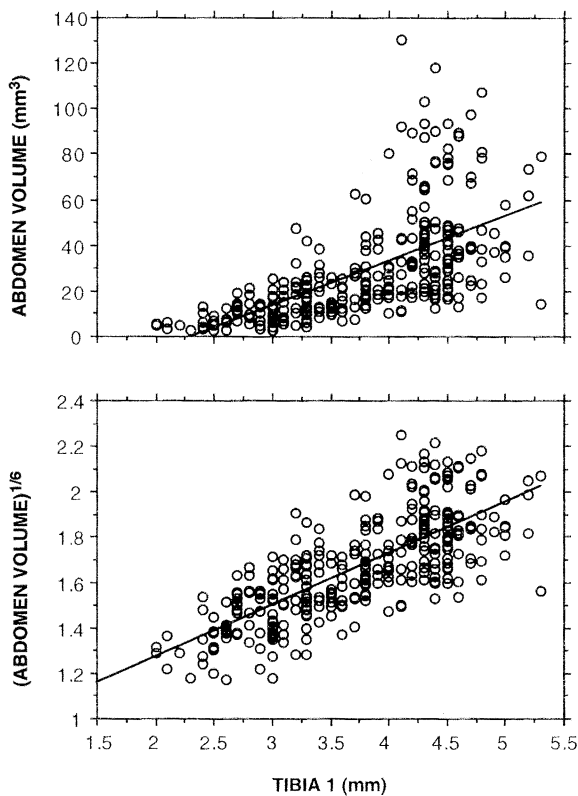


Fig. 1. Top panel. Regression of abdomen volume against tibia length demonstrating increased variance in volume for larger *Metepeira incrassata* spiders (1993 data). Bottom panel. Transformed data. The residuals of points from the regression line form the residual index.

of regression lines from 1993 field-caught spiders and 1993 post-treatment spiders to check the stability of our slope estimate. (3) For the residual index, we regressed abdomen volume ( $\text{mm}^3$ ) against tibia length (mm) for the 1993 data. Variance in abdomen volume increased dramatically in larger spiders (Fig. 1 Top). To homogenize the variance across spider size, we took the sixth root of abdomen volume (Fig. 1 Bottom); other transformations may be appropriate for other data sets (In

transformations were unsuccessful in homogenizing variance in this example). The regression of transformed abdomen volume on tibia length was highly significant ( $r^2 = 0.579$ ,  $df = 1,310$ ,  $P = 0.0001$ ). We then extracted the residuals from this analysis to be used as the condition index for each spider.

We checked the performance of each index in two ways. First, we tested whether the results made sense in light of the feeding regimes imposed on the spiders using analysis of variance. Second, we tested for size bias of each index by checking whether the indices correlated with tibia length, using Pearson's  $r$ . A sound condition index should show significant differences across feeding regimes but no correlation with body size.

## Results

### *Pardosa*

#### Field studies

The two indices used to compare spiders from till vs no-till fields produced different results. Spiders from no-till plots were significantly fatter than those from the till plots based on the ratio index, but the groups did not differ based on the residual index (Table 1). This discrepancy results from the fact that the ratio index did not adequately control for spider size: there was a significant correlation between the ratio index and carapace width ( $r^2 = 0.528$ ,  $df = 51$ ,  $P < 0.0001$ ) and a significant difference in the body sizes of the spiders in the two groups ( $t = 3.88$ ,  $df = 50$ ,  $P < 0.001$ ). In contrast, the residual index did not correlate with carapace width ( $r^2 = 0.02$ ,  $df = 51$ ,  $P = 0.887$ ).

#### Laboratory studies

We found significant differences between high food and low food groups in two of the three indices. (1) Over the eight-week period, the ratio index of the high- and low-fed groups diverged (Fig. 2). At the end of the study, the ratio index of the high-fed group was significantly higher than that of the low-fed group (Table 1).

Table 1. Mean condition indices ( $\pm 1$  SE) for *Pardosa milvina*. Field animals were collected from till and no-till soybean plots. Laboratory data are from spiders reared in the laboratory for eight weeks under two feeding regimes. Treatment groups were compared with a two-tailed  $t$ -test ( $df = 50$  for field data and 20 for laboratory data).

Condition index	No-till	Field data		$t$	$P$
		Till			
Ratio index	$5.113 \pm 0.254$	$7.083 \pm 0.840$		3.008	0.0041
Residuals	$0.004 \pm 0.040$	$-0.012 \pm 0.069$		-0.203	0.8401
Condition index	High food	Laboratory data		$t$	$P$
		Low food			
Ratio index	$7.100 \pm 0.509$	$5.080 \pm 0.361$		3.313	0.0035
Slope-adjusted ratio index	$2.557 \pm 0.122$	$2.220 \pm 0.111$		2.044	0.0543
Residual index	$0.087 \pm 0.045$	$-0.073 \pm 0.053$		2.253	0.0357



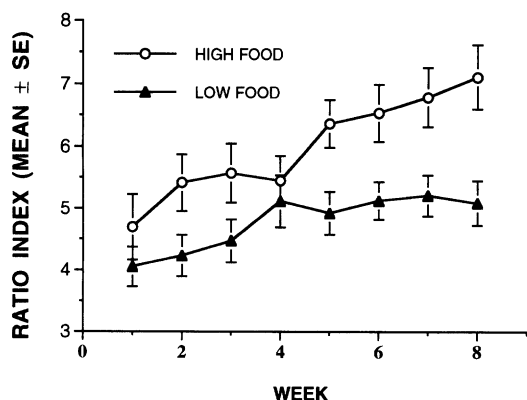


Fig. 2. The ratio index, calculated as mass (mg)/carapace width (mm), for *Pardosa milvina* reared in the laboratory under two feeding conditions.

(2) The regression of  $\ln(\text{body mass})$  on  $\ln(\text{carapace width})$  for field data yielded a best-fit regression line with a slope of  $2.718 \pm 0.212$  (mean  $\pm$  SE,  $df = 51$ ,  $r^2 = 0.767$ ,  $P = 0.0001$ ). The slope-adjusted ratio index for laboratory spiders at the end of the study was calculated with this slope. Though the high-fed group had a larger index than the low-fed group, the difference was not significant at  $P = 0.05$ , though it was very close (Table 1). The slope-adjusted ratio index did not correlate with carapace width ( $df = 21$ ,  $r^2 = 0.0016$ ,  $P = 0.571$ ). The slope of the regression of  $\ln(\text{body mass})$  on  $\ln(\text{carapace width})$  for the laboratory spiders in the last week was less than that of the field spiders (mean  $\pm$  SE:  $2.598 \pm 0.280$ ). (3) The residual index from the regression of  $\ln(\text{mass})$  on  $\ln(\text{carapace width})$  was significantly higher in the high-fed spiders than in the low-fed spiders after eight weeks in the laboratory (Table 1).

### *Meteteira*

All three indices were significantly different across feeding groups in *Meteteira*. However, only the residual index provided a condition estimate that did not correlate with spider size. We present here the analyses from abdomen volumes based on length, width, and depth; results from analyses based on length and width alone were qualitatively identical.

(1) Spiders that were fed more had a higher ratio index (abdomen volume/tibia length) than other spiders ( $P < 0.0001$ , Table 2). This condition index was highly correlated with body size ( $P < 0.0001$ , Table 2).

(2) The slope-adjusted ratio index was calculated by using 1992 data to generate the slope of the regression line of  $\ln(\text{abdomen volume in mm}^3)$  vs  $\ln(\text{tibia length in mm})$  (slope (mean  $\pm$  SE) =  $2.773 \pm 0.096$ ;  $n = 251$ ;  $r^2 = 0.902$ ). The condition index for 1993 post-treatment spiders, calculated with this slope (eq. 1), was significantly affected by feeding regime (Table 2). This index

was not as strongly correlated with body size as the ratio index, but there was a tendency for the slope-adjusted ratio index to increase with body size ( $P < 0.08$ , Table 2).

The slope of the regression line differed across spider populations. In field-caught spiders in 1993, the slope was  $2.63 \pm 0.098$  ( $n = 445$ ), lower than that for 1992. In post-treatment spiders, the slope was higher: in 1992, it was  $3.02 \pm 0.280$  ( $n = 154$ ), and in 1993, it was  $2.97 \pm 0.143$  ( $n = 313$ ).

(3) The residual index was also significantly affected by feeding regime ( $P < 0.0001$ ), but did not correlate with body size ( $P > 0.9999$ ). Thus, this condition index was affected by the feeding regimes in a predictable way (spiders that were fed more had a positive index, and starved spiders had a negative index) and did not behave differently for spiders of different sizes.

### Discussion

We found that the three condition indices generated different results, and only the residual index adequately controlled for variation across body sizes. The ratio index increased with body size in both spider species we tested. Our analyses demonstrate that confounding body size with condition can lead to misinterpretation of data. We found significant differences between ratio indices in *Pardosa* spiders from till vs no-till treatments. However, this difference was traced to body size differences rather than the condition differences that were of interest. In *Meteteira*, there was also a highly significant correlation between body size and this condition index.

We found two problems with the slope-adjusted ratio index. First, the success of this condition index depends on the choice of the standard population used to generate the slope of the regression line, as other authors have pointed out (e.g., Le Cren 1951, Bolger and Connolly 1988). If the slope of the line of the reference population does not adequately fit the data from the study group, this index does not provide accurate information. For *Pardosa*, differences between high and low feeding groups in the laboratory were not detectable at  $P = 0.05$  using this method, though other methods detected a difference. Data from *Meteteira* demonstrate that slopes should not be assumed to be equal, even in samples drawn from the same population in consecutive years: the slope of the regression of  $\ln(\text{abdomen volume})$  versus  $\ln(\text{tibia length})$  for field-caught spiders differed in 1992 and 1993. Differences were even greater between field-caught spiders and those given supplementary food; the range of "fatness" in fed spiders was greater than field-caught animals, and apparently the inclusion of these points at the end of the distribution greatly affected the slope of the line. Thus, our

Table 2. Means ( $\pm 1$  SE) of three condition indices for *Metepeira incrassata*. All three indices significantly differed across feeding regimes (ANOVA). Only the residual index showed no correlation with body size (estimated by tibia length).  $n = 313$  for all tests.

	Capacity	Feeding regime Control	Starved	Significance levels Regime	Correlation with tibia length
Ratio index	10.32 $\pm$ 0.61	6.13 $\pm$ 0.32	4.68 $\pm$ 0.36	$F_{2,310} = 41.13$ $P < 0.0001$	$r = 0.52$ $P < 0.0001$
Slope-adjusted ratio index	0.937 $\pm$ 0.04	0.589 $\pm$ 0.02	0.413 $\pm$ 0.02	$F_{2,310} = 74.12$ $P < 0.0001$	$r = 0.01$ $P < 0.08$
Residual index	0.120 $\pm$ 0.01	-0.018 $\pm$ 0.01	-0.117 $\pm$ 0.02	$F_{2,310} = 94.63$ $P < 0.0001$	$r = 0$ $P > 0.9999$

analyses demonstrate that only when slopes of the regression lines remain constant across samples should this method be used (see also Cone 1989). The second problem with the slope-adjusted ratio index was that it increased with body size in *Metepeira*. Although this correlation was not significant at the 0.05 level, it was strong enough to potentially be of concern. This problem with this index has been pointed out by other authors (Le Cren 1951, Reist 1985).

The residual index had three advantages over the other methods tested, and only one flaw. (1) We found, as did Reist (1985) for morphometric data on fish, that the residual index provided the cleanest way to separate the effects of condition from the effects of body size. Inspection of the residuals provides an easy way to check for homogeneity of variances across body sizes, and to make appropriate transformations of the data when necessary. Statistical packages are readily available that facilitate this process (e.g., Statview 4.0 for the Macintosh, which we used). Inspection of the variance is far preferable to simply assuming that a condition index removes the effects of body size, as is common with the ratio-based indices. The residual index was successful in removing the effects of body size in both our spider species. In *Pardosa*, we found no correlation between the residual index and body size, and thus found no differences in spiders from till vs no-till fields, in contrast to results from the ratio index. Similarly, in *Metepeira*, this index did not correlate with body size ( $P > 0.999$ ). (2) The residual index had a straightforward biological interpretation: spiders with a positive score were fatter than predicted, and spiders with a negative score were thinner than predicted. (3) Appropriately transformed residuals are normally distributed, making further data analysis simpler. However, a flaw of the residual index is that residuals are not comparable across populations. For descriptive purposes, the ratio index yields a number that can be compared across groups.

We recommend that behavioral investigators use the residual method for testing hypotheses about condition differences in animals drawn from the same population, and calculate the ratio index for its descriptive value. In some cases it may be possible to draw meaningful statistical conclusions from the ratio index or slope-

adjusted ratio index if body sizes in the study population do not vary greatly.

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## References

- Anderson, J. F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). – *Ecology* 55: 576–585.
- Baker, R. 1989. Condition and size of damselflies: a field study of food limitation. – *Oecologia* 81: 111–119.
- Bolger, T. and Connolly, P. 1988. The selection of suitable indices for the measurement and analysis of fish condition. – *J. Fish. Biol.* 34: 171–182.
- Clark, C. W. 1991. Modelling behavioral adaptations. – *Behav. Brain Sci.* 14: 85–93.
- Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. – *Trans. Am. Fish. Soc.* 118: 510–514.
- Evans, R. M. and McMahon, B. F. 1987. Within-brood variation in growth and condition in relation to brood reduction in the American white pelican. – *Wilson Bull.* 99: 190–201.
- Gould, S. 1975. Allometry in primates, with emphasis on scaling and evolution of the brain. – In: Szalay, F. S. (ed.), *Approaches to primate paleobiology*. Karger, Basel, pp. 244–292.
- Greenstreet, S. P. R. 1992. Migration of hatchery reared juvenile Atlantic salmon, *Salmo salar* L., down a release ladder. 2. Effect of fish developmental strategy on speed and pattern of movement. – *J. Fish Biol.* 40: 667–681.
- Hagstrum, D. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and field. – *Ann. Entomol. Soc. Am.* 63: 1297–1304.
- Hamer, K. C. and Furness, R. W. 1993. Parental investment and brood defence by male and female great skuas *Catharacta skuua*: the influence of food supply, laying date, body size and body condition. – *J. Zool.* 230: 7–18.
- Harvey, P. and Pagel, M. 1991. *The comparative method in evolutionary biology*. – Oxford Univ. Press, Oxford.
- Hepp, G., Blohm, R., Reynolds, R., Hines, J. and Nichols, J. 1986. Physiological condition of autumn-banded mallards and its relationship to hunting vulnerability. – *J. Wildlife Manage.* 50: 177–183.
- Jakob, E. M. 1991. Costs and benefits of group living for pholcid spiderlings: losing food, saving silk. – *Anim. Behav.* 41: 711–722.

- and Dingle, H. 1990. Food level and life history characteristics in a pholcid spider. – *Psyche* 97: 95–110.
- Juliano, S. 1986. Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). – *Ecology* 67: 1036–1045.
- Külling, D. and Milinski, M. 1992. Size-dependent predation risk and partner quality in predator inspection of sticklebacks. – *Anim. Behav.* 44: 949–955.
- Le Cren, E. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). – *J. Anim. Ecol.* 66: 1504–1512.
- Lucas, A. and Beninger, P. 1985. The use of physiological condition indices in marine bivalve aquaculture. – *Aquaculture* 44: 187–200.
- Mangel, M. and Clark, C. W. 1988. Dynamic modeling in behavioral ecology. – Princeton Univ. Press, Princeton, NJ.
- Marden, J. H. and Rollins, R. A. 1994. Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. – *Anim. Behav.* 44: 949–955.
- Marshall, S. D. and Gittleman, J. L. 1994. Clutch size in spiders: is more better? – *Funct. Ecol.* 8: 118–124.
- Matlack, C. and Evans, A. 1992. Diet and condition of bobcats, *Lynx rufus*, in Nova Scotia during autumn and winter. – *Can. J. Zool.* 70: 1114–1119.
- Moeller, A. 1987. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. – *Anim. Behav.* 35: 1637–1644.
- Morse, D. 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. – *Ecology* 69: 1970–1973.
- Nicoletto, P. F. 1993. Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. – *Anim. Behav.* 46: 441–450.
- Pierce, C., Crowley, P. and Johnson, D. 1985. Behavior and ecological interactions of larval Odonata. – *Ecology* 66: 1504–1512.
- Reist, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. – *Can. J. Zool.* 230: 513–528.
- Renouf, D., Gales, R. and Noseworthy, E. 1993. Seasonal variation in energy intake and condition of harp seals: is there a harp seal morph? Problems for bioenergetic modelling. – *J. Zool.* 230: 513–528.
- Sweitzer, R. and Berger, J. 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). – *J. Mammal.* 74: 198–203.
- Thompson, D. 1942. On growth and form. – Cambridge Univ. Press, Cambridge.
- Thorpe, K. E., Taylor, A. C. and Huntingford, F. A. 1995. How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs, *Necora puber* (L.) (Brachyura, Portunidae). – *Anim. Behav.* 50: 1657–1666.
- Tonn, W. M., Paszkowski, C. A. and Holopainen, I. J. 1989. Responses of crucian carp populations to different predation pressure in a manipulated pond. – *Can. J. Zool.* 67: 2841–2849.
- van Berkum, F., Huey, R., Tsuji, J. and Garland Jr., T. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird and Girard). – *Funct. Ecol.* 3: 97–105.
- van Marken Lichtenbelt, W. D., Wesselingh, R. A., Vogel, J. T. and Albers, K. B. M. 1993. Energy budgets in free-living green iguanas in a seasonal environment. – *Ecology* 74: 1157–1172.
- Watson, P. J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). – *Behav. Ecol. Sociobiol.* 26: 77–90.