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Relationships between condition factors, parasite load and paternity in bluegill sunfish, *Lepomis macrochirus*

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Synopsis

We examined the relationship between non-polar lipid density, parasite density and paternity of male bluegill sunfish, *Lepomis macrochirus*, and four condition factors: (1) Fulton's condition factor, K; (2) the relative condition factor, K_n; (3) the relative mass index, W_r; and (4) the residuals from the geometric regression of mass on total length, C. Although the four factors were highly correlated to each other, only K and W_r were significantly correlated with non-polar lipid density, explaining about 40% and 25% of the variation, respectively. K was also the best predictor of parasite density and was significantly correlated with the paternity of nesting males. These data provide support for K as a good indicator of individual energetic state and overall quality during the breeding period and demonstrate the importance of energetic state for understanding reproductive success in bluegill sunfish.

Introduction

Individual condition is an important component of performance, survivorship and reproductive success in fish (e.g. Forseth et al. 1999). Condition can be defined in energetic terms as the amount of energy available to an individual which may be allocated to various life functions including reproduction, foraging and over-winter survival (Ricker 1975). Condition factors are presumed to reflect the fat content, and ultimately, the amount of energy possessed by an individual, and have been used in the fisheries literature for some time (Bolger & Connolly 1989, reviewed by Cone 1989). More recently, condition factors have been adopted by ecologists studying fish mating systems under the assumption that they reflect an individual's energetic state and overall quality. Condition factors have been successful at explaining variation in reproductive behaviours and success (e.g. Nicoletto 1995, Barber 2002, Kondoh & Okuda 2002). However, few studies have examined the link between condition factors and energetic state or other measures of quality at the onset of breeding when information on individual condition is required to understand variance in mating and reproductive behaviours.

There are four primary condition factors, all of which are based on length–mass relationships (Cone 1989). First, Fulton's condition factor, K, represents the mass of an individual relative to its body length. K assumes isometric growth in which mass scales to the cube of length (Schmidt-Nielsen 1984). Second, the relative condition factor, K_n (LeCren 1951), is an extension of K that was formulated to account for the violation of the assumption of isometric growth. K_n is instead based on a scaling power (other than 3) that is derived directly from the population sample. It is assumed that the population scaling pattern reflects the true allometry between length and mass (Cone 1989). Third, the relative mass index, W_r (Wege & Anderson 1978), examines the mass of an individual relative to a standard mass generated from species-specific biometric characteristics. W_r assumes that differences among populations in the mass–length relationship reflect environmental and not genetic factors. Thus, by examining multiple populations the true allometry for the species can be derived. Fourth, the residuals from a geometric linear regression of the logarithm transformed values of mass and length, C, have been used to estimate condition. An individual with a positive residual lies above the regression line and is heavier than expected for its length and has high condition, while an individual with a negative residual has low condition.

These four condition factors are all based on the premise that heavier fish of a given length are in a higher energetic state. In fish, non-polar lipid density is typically used as a measure of an individual's energetic state because it is the main energy source utilized during periods of starvation, reproduction, and maturation (Wootton et al. 1978, Reznick & Braun 1987, Norton et al. 2001). Several studies have confirmed a relationship between K or K_n and non-polar lipid density, including in three-spined stickleback *Gasterosteus aculeatus* (Chellappa et al. 1995), striped bass *Morone saxatilis* (Gershanovich et al. 1984, Brown & Murphy 1991), broad whitefish *Coregonus nasus* (Fechhelm et al. 1995), ship sturgeon *Acipenser nudiventris* (Gershanovich et al. 1984), muskellunge *Esox masquinongy* (Jonas et al. 1996), and Atlantic salmon *Salmo salar* (Pinder & Eales 1969, Herbinger & Friars 1991, Kadri et al. 1995). However, Simpson et al. (1992) and Sutton et al. (2000) showed that in Atlantic salmon, the strength of the correlation between the condition factors and lipid density varied during the season, stressing the importance of determining an association at critical periods, such as at the onset of breeding for studies of mating systems and reproductive success.

This paper evaluates the ability of four condition factors to predict non-polar lipid density of bluegill sunfish caught at the onset of the breeding season. Next, it examines the relationship between the condition factors and parasite density as another measure of individual quality. Finally, it examines the relationship between individual quality and paternity (proportion of young fertilized by a male) in a naturally breeding colony.

Study species

The bluegill is native to lakes and rivers of North America (Lee et al. 1980). Males exhibit a polymorphism in life history and behaviour termed 'parental' and 'cuckolder' (Gross 1982). In Lake Opinicon, Ontario (44°34′N, 76°19′W). Parental males delay maturation for about 7 years and then compete for preferred territories in nesting aggregations during their May–July breeding season. Parental males spawn with multiple females over the course of a single day and then provide care for 7–10 days: embryos hatch 2–3 days after fertilization and the young remain in the nest for up to 7 more days. In contrast, cuckolder males mature precociously at about 2 years and do not compete for territories, build nests, or associate with young. Instead, cuckolders steal fertilizations by either mimicking female behaviours to gain access to nests or sneaking into nests when a pair spawning is about to occur. In this study we focus on parental males.

Methods

Lipid analysis

We captured 21 parental males from Lake Opinicon by seine during the third week of May 1994. We measured total body length, L_T (mm, tip of jaw to extended caudal fin), and wet body mass, W (g), of each male at the time of capture. We the wrapped the fish individually in tin foil and immediately froze them (−20°C). We measured the volume of non-polar lipids in each individual 1 month after collection following established protocols (see Cargnelli & Gross 1997). In brief, we ground each fish into a homogenous mixture, and soaked the homogenate in a 1:1 solution of hexane and dichloromethane for approximately 90 min. We evaporated the solvent using a rotoevaporator, leaving only lipids in the bottom of a pre-weighed flask, from which we determined the total mass of lipids (W_L).

We next examined lipid density calculated from lipid mass divided by body mass minus lipid mass (hereafter referred to as 'non-polar lipid density'). We also adjusted the lipid mass for individual metabolic rate by dividing lipid mass by body mass (minus lipid mass) raised to the power of 0.8. The coefficient represents the suggested allometry between body size and metabolic rate in fishes (Brett & Groves 1979, Post & Evans 1989, Shuter & Post 1990, but see Riisgård 1998, Schultz & Conover 1999) and should provide a better measure of individual energetic state than non-polar lipid mass adjusted solely for body mass. Hereafter, we refer to this adjusted value as 'adjusted non-polar lipid density'.

We estimated the condition of each fish in the sample using the following four indices: (i) Fulton's condition factor: $K = W/L_T^3 \times 10^6$ (Ricker 1975). (ii) Relative condition index: $K_n = W/W_E \times 100\%$, where W_E is the length-specific expected mass predicted from the mass–length regression for the population (LeCren 1951). We calculated the length–mass relationship for the Lake Opinicon bluegill population using a geometric linear regression from a 5 year sample (1988–1993) of parental males collected throughout the months of May to September and it was $\log_{10}W_E = -5.97 + 3.532 \log_{10}L_T$ ($r^2 = 0.69$, $n = 901$, $p < 0.001$). (iii) Relative mass index: $W_r = W/W_S \times 100\%$, where W_S is the length-specific standard mass predicted by a mass–length regression for the species as a whole. The standard mass equation for bluegill developed by Hillman (1982) is $\log_{10}W_S = -5.374 + 3.316 \log_{10}L_T$. (iv) Standardized residuals: C was calculated from the residuals from a geometric linear regression of $\log_{10}W_S$ onto $\log_{10}L_T$ for our sample.

Paternity and parasite analysis

We collected 38 parental males from a naturally breeding colony in Lake Opinicon at the end of the parental care period in June 1996. Details of the colony can be found in Neff (2001). We collected a random sample of young from each male's nest and preserved them in 95% ethanol for microsatellite DNA analysis of paternity. The paternity results were reported by Neff (2001). Briefly, we obtained genotypes from each male and from an average of 44 young from each brood (range = 31–46). In total, we generated approximately 18 000 genotypes using 11 microsatellite loci. We then calculated paternity for each male using the two-sex paternity model presented in Neff et al. (2000). This model accounts for the resolving power of the loci and calculates the proportion (0–100%) of young that are genetic offspring of the nest-tending parental male. We arcsine square-root transformed paternity for all analyses to remove mean-dependent variance.

We quantified parasite density of each parental male based on counts of five parasite types obtained through complete dissection of the fish: *Dactylogyrus* sp., *Ergasilus caeruleus*, *Proteocephalus* sp., *Spinitectus* sp. and *Leptorhynchoides* sp.. We could not always identify parasites definitively to species. We selected these parasites because they are known to be prevalent in bluegill and they actively feed on their fish host (as opposed to being in a dormant, cyst state: Hoffman 1967, Muzzall & Peebles 1998). Haemoflagellate parasites are rare in bluegill and we did not analyze them (Muzzall & Peebles 1998). We calculated parasite density as parasite number divided by host body mass. Next we calculated an adjusted

Table 1. Intensity (mean number and range per individual), and percent of the total parasite number or mass of five parasite types in bluegill sunfish.

Parasite	Intensity	% By number	% By mass
Dactylogyrus sp.	0.56 (0–3)	5.5	3.8
Ergasilus caeruleus	0.19 (0–1)	1.8	1.7
Proteocephalus sp.	0.70 (0–5)	6.8	10.9
Spinitectus sp.	7.56 (0–41)	73.2	12.5
Leptorhynchoides sp.	1.30 (0–9)	12.7	71.1
Total	10.3 (0–46)	100	100

The data are based on dissections of 38 nest-tending parental males.

parasite density based on the total mass of parasites (as opposed to the number). We first converted parasite number to mass by multiplying the number of parasites by their estimated average mass. We calculated the adjusted parasite density from the estimated mass of all parasites divided by the host body mass (Table 1). We incorporated parasite mass into the calculation because mass is expected to better represent the potential energetic cost of the parasite to the host (Muzzall & Peebles 1998).

Results and discussion

The four condition factors were highly correlated with each other, but varied considerably in their relationship with non-polar lipid density, parasite density and paternity in bluegill (Table 2). Only Fulton's condition factor, *K*, and the relative mass index, W_r, were significantly correlated with non-polar lipid density. There was only a small effect on these relationships when the potential metabolic allometry was incorporated into the calculation of non-polar lipid density; although in all cases the correlations were stronger. Overall, *K* was the best predictor of lipid density, explaining about 40% the variation among individuals (Figure 1a). *K* also was most highly correlated with parasite density (Figure 1b) and significantly correlated with paternity (Figure 1c). *C* was most highly correlated with paternity, albeit only marginally more so than *K*.

One potential difficulty with *C* is that an individual's index is defined relative to the group of individuals used in the geometric regression. Thus, when the group composition changes, an individual's index can change as well. For example, we initially calculated *C* for our parental males separately for the two groups (i.e., the group collected for the lipid analysis (n = 21) and the group collected at the end of the parental care period (n = 38)) and then a second time for the two groups combined (n = 59). We found that the two *C* estimates for each individual were highly correlated ($r = 0.86$, n = 59, $p < 0.001$), but when analyzed in the combined sample the individuals collected for the lipid analysis had significantly higher *C* values (paired *t*-test: $t_{20} = 2.86$, $p = 0.010$), while the individuals collected at the end of the care period had significantly lower *C* values (paired *t*-test: $t_{37} = -5.85$, $p < 0.001$). It is possible that these differences are due to the fact that parental males do not actively forage during the parental care period and can expend considerable energy (Gross 1982, Coleman & Fischer 1991). Nevertheless, *C* typically will be less comparable among different samples of fish (and thus across studies) than the other three factors.

Table 2. Pearson correlation coefficients for comparisons between four condition factors and non-polar lipid density and adjusted non-polar lipid density, parasite density and adjusted parasite density, and paternity in bluegill sunfish.

Condition factor	K_n (21, 38, 59)	W_r (21, 38, 59)	C (21, 38, 59)	Lipid density (21)	Adjusted lipid density (21)	Parasite density (38)	Adjusted parasite density (38)	Paternity (38)
K	0.725^a 0.976^a 0.726^a	0.917^a 0.991^a 0.809^a	0.690^b 0.969^a 0.960^a	0.582^b	0.622^b	-0.372^d	-0.548^a	0.399^d
K_n	–	0.940^a 0.997^a 0.988^a	0.930^a 0.920^a 0.865^a	0.311^c	0.316^c	-0.287^c	-0.514^b	0.317^c
W_r	–	–	0.882^a 0.994^a 0.929^a	0.470^d	0.493^d	-0.360^d	-0.530^b	0.350^d
C	–	–	–	0.238^c	0.241^c	-0.342^d	-0.535^a	0.411^d

The three coefficients for each of the comparisons between the condition factors are based on, from top to bottom, the fish sample collected for lipid analysis, the sample collected from the breeding colony, and the combined sample. The numbers in parentheses are sample sizes.

Statistical significance: $^a p < 0.001$, $^b p < 0.01$, $^c p > 0.05$, $^d p < 0.05$.

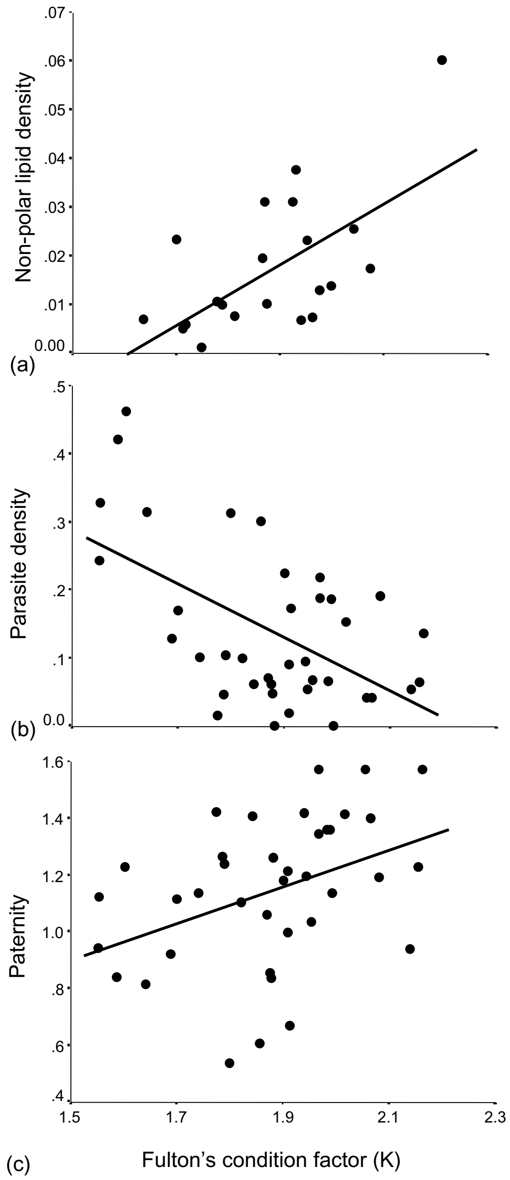

Figure 1. The relationship between Fulton's condition factor (*K*) and non-polar lipid density (adjusted) (a), parasite density (adjusted) (b), and paternity (c) in bluegill sunfish. Statistical results are presented in Table 2.

Among the 38 nest-tending parental males we collected from a naturally breeding colony, the mean intensity of the five parasite types ranged from an average of 0.2–7.6 per individual (Table 1). These intensity data are comparable to other bluegill populations (Muzzall & Peebles 1998). In our sample, *Leptorhynchoides* sp. was the largest parasite and represented 71% of the total mass of parasites. *Spinitectus* sp. had the highest intensity at 73% by number, but because it was considerably smaller than the former parasite, it represented only 13% of the total mass of parasites.

In all cases, the adjusted parasite density, which accounted for the mass of each parasite, was more highly correlated with the condition factors than were the unadjusted values, which were based on parasite numbers. These data suggest that parasite mass better reflects the energetic cost of the parasites to the host than does parasite number. Furthermore, the adjusted parasite density values were correlated with paternity ($r = -0.34$, $n = 38$, $p = 0.037$), but the unadjusted values were not ($r = -0.23$, $n = 38$, $p = 0.18$).

Stepwise multiple linear regression of K and adjusted parasite density on paternity revealed that only K had an independent significant effect (K: $\beta = 0.40$, $t_{36} = 2.61$, $p = 0.013$; Parasite density: $\beta = -0.18$, $t_{36} = -0.95$, $p = 0.35$). This analysis suggests that parasites might affect paternity indirectly, through their effect on energetic state, but not directly. Because parental males actively defend their nest from intrusions by cuckolder males during spawning, it is likely that parentals with less energy are less able to thwart intrusions. In sticklebacks, parasite infection by *Pomphorhynchus laevis* (Acanthocephala) has similarly been reported to be negatively correlated with energy reserves and subsequently reproductive success (Bakker & Mundwiler 1999). The Acanthocephala (*Leptorhynchoides* sp.) was the predominant parasite by total mass in our study.

Interestingly, of the four indices, only K was positively correlated with a parental male's length ($r = 0.62$, $n = 21$, $p = 0.003$) and mass ($r = 0.75$, $n = 21$, $p < 0.001$), indicating that this index may not be independent of body size. Thus, K may capture an individual's energetic state as well as other factors that relate to body size. For example, in our colony we found that heavier males obtained higher paternity ($r = 0.43$, $n = 38$, $p = 0.007$), and this may contribute to the observed relationship between K and paternity.

We used total body length in our calculations of the condition factors. It is unlikely that using standard length (i.e., total body length less caudal fin length) would have any significant effect on our analysis because the two measures are highly correlated in bluegill. For example, in a sample of adults, which comprised females, parental males and cuckolder males, collected at the onset of the breeding season in Lake Opinicon, the correlation between total and standard lengths was $r = 0.998$ ($n = 204$, $p < 0.001$; data not shown). In other species, however, differences may arise, particularly when the caudal fin is under directional selection (e.g., Meyer 1997, Karino & Haijima 2001). In this case, using total length could lead to less accurate inference about condition when individuals in good condition produce relatively larger caudal fins (which would reduce their condition factor). Thus, using standard length generally may be more reliable.

Several other studies have revealed relationships between condition factors and parental behaviour and reproductive success. For example, in the sand goby, *Pomatoschistus minutus*, males with higher K_n were more dominant and were preferred by females (Barber 2002) and food addition experiments showed that males with increased energy reserves spent more time at their nests caring for the young (Lindström 1998). In the common goby, *Pomatoschistus microps*, males with higher K_n were less likely to cannibalize their broods (Kvarnemo et al. 1998).

In summary, using condition factors as a measure of individual energetic state is convenient because they can be easily calculated using non-invasive techniques. Of the four measures examined here, K provided the best estimates of individual non-polar lipid density at the onset of breeding and was correlated with both parasite density and paternity in bluegill sunfish.

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