

Reproductive investment of giants and dwarfs: specialized tactics in a cichlid fish with alternative male morphs

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Summary

1. Adopting alternative reproductive tactics may require divergent solutions to reproductive competition among individuals of a population. Often investment in reproduction differs substantially between individuals pursuing bourgeois and parasitic tactics, which may result in different trade-offs and limitations.

2. Here we identify divergent behavioural, morphological and physiological traits of bourgeois and parasitic male morphs in *Lamprologus callipterus*, a Lake Tanganyika cichlid with an extreme size dimorphism among males. We focus on limiting factors and compare these between large, nest-building males and dwarf males parasitizing their reproductive effort.

3. Only nest males invest in courtship, and they exhibit much more aggression than dwarf males. In contrast, dwarf males spend 20% of their time feeding, whereas nest males hardly ever feed.

4. Nest males accumulate reserves before breeding and use these up before taking a reproductive break, thereby performing a 'capital breeder' strategy. In contrast, dwarf males use assimilated energy immediately for reproduction, thus acting as 'income breeders'. This is a requirement of their spawning tactic, which only works out with a small and slim body.

5. A field experiment showed that nest males lose weight by their restricted feeding opportunities while holding a nest, which would allow them to hold a territory for 103 days on average. Due to their reproductive investment, however, they held territories only for a mean period of 33 days, which reveals the relative importance of opportunity costs and reproductive expenditure.

6. Nest males are also limited by the requirement to fertilize each egg of a clutch with a separate ejaculate. Their ejaculation rate and the number of sperm released both decline sharply after 5 h, whereas undisturbed spawning lasts 2–4 h longer than that.

7. There is a strong allometric relationship between body mass and gonad weight, with smaller males of both tactics investing disproportionately more in testes than large males. The major limitation of dwarf males is apparently access to spawning females, which is prevented by the monopolization of nest owners and becomes more difficult with increasing size of dwarf males.

8. Our results show that different males in a population may act as capital or income breeders depending on tactic and may face very different limitations, which is a direct result of highly divergent spawning tactics and resulting body sizes.

9. We argue that capital and income breeding are useful concepts to understand divergent life history decisions associated with alternative reproductive tactics, i.e. behavioural polymorphisms within a species and within one sex. It might turn out that in general, bourgeois tactics rather adopt a capital breeding strategy whereas parasitic tactics are inclined to perform as income breeders, due to the diverging constraints faced by these types of reproduction, although we discuss possible exceptions.

Key-words: alternative reproductive tactics, bourgeois males, capital breeding, cichlid fish, income breeding, *Lamprologus callipterus*, sperm competition, Lake Tanganyika

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Introduction

Within a species natural and sexual selection mechanisms may push male and female body sizes in opposite directions and towards extreme levels (Parker 1992; Vollrath 1998; Schütz & Taborsky 2003, 2005; Schütz *et al.* 2006; Fairbairn, Blanckenhorn & Székely 2007). Extreme sexual size dimorphisms (SSDs) may facilitate the evolution of alternative reproductive tactics (ARTs) within the larger sex, because surviving to maturity takes a long time and is hence unlikely, causing some individuals to benefit from maturing early and acting as reproductive parasites (Taborsky 2001). In consequence, an intrasexual dimorphism may evolve with bourgeois individuals adopting a capital breeding strategy based on accumulating reserves for reproduction, and parasitic individuals reproducing early by acting as opportunistic income breeders.

Among vertebrates, fish show the greatest variability of alternative reproductive tactics in the male sex (Taborsky 1994, 2008; Avise *et al.* 2002; Mank & Avise 2006). Usually, bourgeois males that attempt to monopolize females are exploited by conspecific male competitors parasitizing their reproductive investment. The crucial distinction between these ARTs is their fundamentally different reproductive effort. Energy expenditure caused by behavioural, morphological and physiological effort entails generally much higher costs on bourgeois than on parasitic males (Taborsky 1994, 2008). Bourgeois males invest either in direct defence of mates, in monopolizing resources for females, or in displaying traits that attract females because they signal male quality. Parasitic males exploit the reproductive investment of bourgeois males by attempting to fertilize eggs quickly (streaking) or inconspicuously (sneaking; Gross 1982; Taborsky 1997).

Adaptations of bourgeois and parasitic tactics to reproductive competition are usually divergent and often contrary to each other (Gross 1982; Taborsky 1997, 2008; Oliveira, Taborsky & Brockmann 2008). At the behavioural level, bourgeois males often attempt to monopolize reproduction by defending a territory or mating site, which provides females with shelter, food, or breeding substrate (Kuwamura 1986; Sato & Gashagaza 1997; Taborsky 2001). In contrast, reproductive parasites benefit from an inconspicuous or swift performance that is confined to the act of spawning (Gross 1982; reviewed in Taborsky 1994). Morphological investment of bourgeois males includes the acquisition of large body size, conspicuous signals such as gaudy colouration or body appendices, and the development of weapons that increase fighting potential, such as the hooknose in salmon (Tchernavin 1938; Jones 1959). In parasitic males, small rather than large body size often increases the fertilization potential, because small males are less conspicuous, more mobile and harder to pursue (Gross 1982). In contrast, large testis size is an adaptation of parasitic males to sperm competition reflecting high energetic investment. Parasitic males typically have larger testes in relation to their body size than bourgeois males (Gage, Stockley & Parker 1995; Awata *et al.* 2006), because they are subject to sperm competition to a much

higher degree than bourgeois males (Parker 1990; Petersen & Warner 1998; Taborsky 1998, 2001; however, see Tomkins & Simmons 2002 for a cautionary note). Physiological investment of bourgeois males involves the production of hormones (Brantley, Wingfield & Bass 1993) and possibly pheromones (Jonge, Ruiter & Hurk 1989; Resink *et al.* 1989), and it is generally characterized by an increased energy expenditure caused by investment in mate acquisition and brood care. This may reduce growth or body condition and thereby limit the time bourgeois males can be reproductively active (Sato 1994). In contrast, allocation of energy towards sperm production is the main way in which parasitic males can raise fertilization probability (Parker 1990).

The way individuals compensate for the resource demands of reproduction is an important cause of life-history variation (Jonsson 1997; Koivula *et al.* 2003). Some organisms fuel their reproductive expenditure from energy gained earlier and stored prior to use ('capital breeders'), whereas others fuel it by feeding when they are reproductively active ('income breeders', Bonnet, Bradshaw & Shine 1998; Bonnet *et al.* 2001). For example, many large mammals are capital breeders, where body weight fluctuates strongly with season and year and relates to reproductive success reciprocally (Festa-Bianchet, Gaillard & Jorgenson 1998). In contrast, small mammals have been considered typical income breeders (Koivula *et al.* 2003), where body weight varies on a much shorter time scale (Andersen *et al.* 2000).

In *Lamprologus callipterus* (see Fig. 1), a shell brooding cichlid from Lake Tanganyika, two very distinct male life histories co-exist within a population. Among all animals, this fish species shows the most extreme sexual size dimorphism (SSD) with males being bigger than females (Schütz & Taborsky 2000, 2005; Schütz *et al.* 2006), which may favour the evolution of ARTs (Taborsky 2001). Indeed, in *L. callipterus* the two alternative male morphs differ extremely in their body size, behaviour, and reproductive performance (Taborsky 2001; Sato *et al.* 2004). Bourgeois males, hereafter referred to as nest males, are on average more than 12 times heavier than females (Schütz & Taborsky 2000). They construct nests of empty snail shells and defend them against competitors (Sato 1994; Maan & Taborsky 2008). Females enter a shell in a nest for spawning and care for the brood within this shell by guarding and fanning eggs and larvae for 10–14 days. During



Fig. 1. *Lamprologus callipterus* nest male in spawning position over a snail shell containing an egg laying female.

this time males hold the territory which they cannot leave and they rarely feed. Due to condition decrease during territory maintenance, their time to hold a territory seems to be limited (Sato 1994). Before reaching the size at which males can compete for nests, they may behave as sneakers by entering a territory during spawning to fertilize eggs while the nest owner is inattentive. This tactic is opportunistic and transitional, and occurs typically before the switch to nest male behaviour (Taborsky 2001).

Males of the second life history pathway halt growth long before reaching female size ('dwarf males'). They attempt to enter shells in which females are spawning by wriggling past them towards the tip of the shell, from where they attempt to fertilize the eggs ('wriggling tactic'; Taborsky 1998, 2001; Sato *et al.* 2004). These dwarf males often move on their own or in small groups visiting different territories, where they may also sit and wait for opportunities of reproductive parasitism. They may occasionally sneak fertilisations, similar to medium sized sneaker males of the bourgeois type ('mouthing tactic'; Sato *et al.* 2004). The bourgeois and dwarf male pathways are fixed for life and reflect a Mendelian genetic polymorphism (Wirtz 2008). Within a population, the two tactics are probably maintained by frequency dependent selection, causing both tactics to render equal payoffs at equilibrium (Gross 1996; Brockmann & Taborsky 2008).

The aim of this study was to unravel the reproductive trade-offs and the different reproductive investment strategies of nest males and dwarf males, i.e. individuals adopting alternative life history pathways. These males differ extremely in size, with dwarf males weighing on average only 2.5% of nest males (Sato *et al.* 2004), which greatly affects their potential to accumulate reserves for reproduction. Koivula *et al.* (2003) pointed out, that 'it is necessary to study trade-offs in the wild, where individuals face both the ecological and physiological costs of reproduction'. By comparing the reproductive effort patterns between nest and dwarf males in the field we examined whether nest males are behaving as 'capital breeders' and dwarf males as 'income breeders'. We hypothesized that due to the requirement to defend a nest site continuously during breeding and hence reduced feeding opportunities, nest males must store much more energy for reproduction than dwarf males, and that the time nest males can hold a territory is constrained by their condition decrease when fasting. We expect nest males to be limited also at the level of sperm production, as they have to fertilize each egg with a separate ejaculate in this species (Bachar 2002), and they often face sperm competition with ejaculates of parasitic males. Due to their small size and limited storage capacity, dwarf males should continue to feed during reproduction instead of living from reserves. Their main reproductive constraint might be a small absolute testis size due to their small body size, and limited access to females due to the nest males' monopolization. In accordance with substantial differences in resource holding potential, we expect nest males to expend more time and effort in aggression than dwarf males.

To test these hypotheses, at the behavioural level we recorded time budgets to measure the time spent with repro-

ductive activities and feeding, and with other activities. At the morphological level, we determined the patterns of energy allocation in somatic and gonadic growth. At the physiological level we searched for possible somatic and gonadic limitations in reproduction. We conducted a field experiment to estimate the rate of condition decrease during fasting in nest males in order to determine the limit for territory maintenance as caused by feeding restrictions, and investigated sperm allocation of nest males in a lab experiment. For dwarf males, we determined how often they are able to dart into a nest during spawning of the nest males in the field.

Materials and methods

BEHAVIOUR AND TIME BUDGETS OF NEST AND DWARF MALES IN THE FIELD

We made focal watches of 16 nest males defending a territory, and of 15 dwarf males found in the vicinity of these territories in Lake Tanganyika at Wonzye Point, Zambia, in January and February 1998. Their behaviour was recorded every 10 s over a period of 10 min each, using the following categories: (1) *Being inactive*, when the focal male remains immobile above the ground in the water column or sits immobile on the bottom. (2) *Feeding*, when the focal male feeds by picking up a mouthful of sand in search of food, which is usually followed by releasing the sand through the opercula and mouth. (3) *Courtship*, consisting of (i) zigzag swimming, when the male performs a series of fast and sharp turns in the vicinity of a female, (ii) pushing and restrained biting of the female, (iii) head-jerking in front of the female (shown mostly near a shell entrance), (iv) agitated shell manipulation, when the male touches and moves the shell with his mouth in front of a visiting female, and (v) sniffing movements towards a female in a shell, when he opens and closes his mouth and opercula, probably to suck up water. (4) *Aggression*, consisting of (i) fin display directed against fish of other species or other nest males by spreading the dorsal fin, and (ii) chasing of conspecific males or females, or fish of other species. (5) *Other behaviours*, which consisted of (i) swimming, (ii) shell manipulation, when a shell is pushed, turned, carried or thrown over by the territory owner, (iii) fleeing, when the male flees from the aggression of others, and (iv) spawning, when the male places his genital papilla over the shell entrance and stays immobile for one to 4 s, during which time ejaculation takes place (Sato 1994; Pachler 2001). We compared the effort spent with these behaviours between nest males and dwarf males using Mann-Whitney *U*-tests. We used non-parametric statistics because some behaviours did not occur during the observations in one or the other male type, so the variances differed between the samples. All statistical tests used two-tailed probabilities.

BODY RESERVES AND TESTES

We determined gonad free condition factors (GF_{CF}) for nest and dwarf males in the field [GF_{CF} = Soma WT (g)/Standard length³ (m³), where soma weight = Body weight (g) – Gonad weight (g); c.f. Sutton, Bult & Haedrich 2000; Neff 2003; Oliva-Paterna, Vila-Gispert & Torralva 2003]. In an earlier study (Schütz *et al.* 2006), we reported gonado-somatic indices [gonad weight/(body weight × 10)] for the two male types. From the same samples we now determined GF_{CF} as a measure of the relative investment in body reserves and gonads. We dissected 29 nest males and 51 dwarf males to determine their gonad

weights (GWT, mg). We also calculated the percentage of gonad weight from body weight and compared it between nest and dwarf males.

Since there is an allometric relationship between soma mass and gonad mass (see Tomkins & Simmons 2002; Stoltz, Neff & Olden 2005), we tested whether the slopes of the relationship of $\log_{10}(\text{GWT})$ and $\log_{10}(\text{Soma WT})$ differ between nest and dwarf males, or whether they are homogenous. Following Tomkins & Simmons (2002), homogeneity of variance was examined with ANCOVA from the interaction term between mating tactic and the covariate $\log_{10}(\text{Soma WT})$.

LIMITS TO REPRODUCTION

Condition decrease of nest males by reduced food access

Nest males cannot leave their nests without losing them, so they have very limited feeding possibilities. To check for the mere effect of spatial restriction (i.e. a reduced feeding range) on their body condition, i.e. without the effect of investing in reproduction, we kept 43 territorial males between 9.0 and 11.7 cm standard length (SL) in underwater cages with a natural sand bottom. As the cage bottom was open these males had access to their natural food source; they feed mainly on shrimps (family Atyidae) that move through the sand (Yuma 1994). The area they had available for feeding was comparable to the size of a nest (1 m²). This study was conducted at Kasakalawe Bay at 8 m depth from February to April 1997. The males were measured at the beginning of the experiment (SL and weight, WT) and then every other week for a period of less than 50 days (10–49 days for individual males). We calculated the average condition decrease per day (ΔC) for every male, where $C = \text{WT}/\text{SL}^3$ in g cm⁻³, and checked whether the condition decrease is related to body size.

For an estimate of the condition at the start and end of the nest holding period we randomly caught 52 active nest males, not knowing their nest holding periods, to determine their SL and WT. We assumed that condition decrease during territory maintenance is the limiting factor determining the territory holding period. Nest males with a high condition factor have probably just started to become territorial, and males with a low condition factor have probably defended their nests already for a long time. The males were divided in three size classes (9–10 cm SL: $N = 35$; 10.1–11 cm SL: $N = 13$; > 11 cm SL: $N = 4$). From each size class we calculated the minimum and maximum condition factors, and the difference between them. The mean of these three condition differences was used as an estimate for the average condition decrease during territory maintenance.

Nest holding period

To estimate the average duration of the territory holding period of nest males in the field, we determined the average proportion of nest owners that deserted their nests per day. Since catching and fin clipping of nest owners sometimes caused conflict with neighbours and resulted in shell stealing, we abstained from marking nest owners and attempted to recognize them by natural markings like scars and natural cuts in their fins. This worked out for about one third of the nest males, so between 16 and 29 nest males were individually recognizable at any given time during the monitoring period from February to April 2003. All nests with recognizable owners were checked daily for continued owner's presence. If a nest was not checked for one or a few days in succession and the nest owner was no longer present afterwards, we assigned the same probability of nest abandonment to each of the days the nest was not monitored. As nest abandonment might

vary with the lunar cycle, the proportion of males that abandoned their nest was determined for all days of a full lunar cycle.

Ejaculation rate and spawning duration of nest males

In a laboratory experiment in 2000, 420 L tanks were divided into two differently-sized (1 : 2) compartments with a clear Plexiglas partition. The tanks were visually separated from the rest of the room by a dark cover to prevent the fish from being disturbed by the observer. We surveyed the experimental tanks with a video-camera from the time of releasing the fish into the tank until the end of mating. The bigger compartment was set up as a territory for a large male, and five manipulated shells were secured in a position that enabled us to videotape any activity in front of or above them.

In eight replicates of this experiment, a male was combined with a group of four females each. Before introducing the females into the experiment, they were kept without males in holding tanks for a period exceeding three weeks to ensure that they were ready to spawn at the beginning of each replicate. Females that spawned successfully in this experiment were not used again in further replicates, so that each test male spawned with a different female. All fish were measured (SL, WT) and marked individually by injection of black ink into scale pouches at different positions on the body (see Schütz & Taborsky 2005). Before starting the experiment we put the four females in the bigger compartment (with the shells) and the territorial male in the smaller compartment for at least 1 week, so that he was able to see the females but could not interact with them physically. This ensured that both, males and females were ready to spawn when the experiment began. At the beginning of each replicate (each day at 9:00) we transferred the male from the small to the large compartment containing the females and started recording. If the fish had not started to spawn by 12:00, the trial was stopped and started again on the next day to ensure that the fish had at least 8 h of daylight left to complete spawning. When a fish showed no signs of being reproductively motivated it was removed from the experiment and replaced by a corresponding alternative candidate.

To collect the sperm released by the test male, shells were prepared by attaching a silicone tube (inside diameter = 2 mm) to a hole drilled into the first spiral of the shell, close to where the eggs are usually placed during spawning. Water samples of 30 mL each were taken via this tube when the male positioned his genital papilla over the opening of the shell to release sperm. The amount of water contained in the tube itself was 5 mL and the mean shell-volume was 15.4 ± 0.84 mL (mean \pm SD). We took 30 mL samples to ensure that the tube was emptied completely by each extraction. The water sample was immediately mixed with the same amount of 0.1 M phosphate buffer to release the osmotic pressure on the sperm head. All samples were then analysed for the presence and quantity of sperm using methods described by Shapiro, Marconato & Yoshikawa (1994), modified to our needs as follows. After extraction, two drops of Rose Bengal were added for staining the spermatozoa heads. Then the sample was passed through a millipore filter (0.22 μm pore size) under vacuum. The filter paper was dried and cleared with immersion oil. The number of sperm was counted under a light microscope at a magnification of 400 \times in an area of 0.185×0.185 mm, and the count was repeated 20 times on randomly selected portions of the filter. The mean value of these readings was used to estimate the total number of sperm present in the sample (total filter area = 160.61 mm², therefore the sperm count was multiplied by 4692.65). Water-samples were taken of spawning events at intervals of about 10 min, and of these samples one in every half-hour was analysed as described above.

Permanent video recordings were taken of every replicate from the time the male was introduced into the experimental compartment until the end of spawning. We measured the amount of time the territorial male placed his genital papilla above the shell entrance during ejaculation for each water-sample that was analysed, the total number of discrete ejaculations, and the time it took from the start of the experiment until the first ejaculation. We also recorded the period of time between the first and last ejaculation (i.e. spawning duration) and the frequency of ejaculations for each hour of spawning.

To determine the average spawning duration of nest males in the field, seven nests of territorial *L. callipterus* males at Wonzye-Point (1995) and four nests at Kasakalawe Bay (1997) were continuously recorded via underwater video-cameras from new moon to 1 week after full moon during two field seasons (23 November 1995–9 December 1995 and 27 December 1996–30 January 1997). All video recordings covered the whole daylight period (6:00 h–18:00 h), and thereby we were able to determine complete spawning durations of 29 females from ten nests. Spawning activity at night was very low, with only one spawning event in seven nests during a period of three weeks (P. Grubbauer, G. Pachler, D. Schütz, M. Taborsky, unpublished data).

Mating access of dwarf males

To determine how often dwarf males are able to enter a nest and spawn with a female, we focally observed randomly chosen focal dwarf males at 35 nests, where dwarf males were encountered in the nest vicinity (average observation duration 42.8 ± 17 min) until the male was lost out of sight or diving time expired. We noted whether dwarf males (i) approach the nest, i.e. a very slow approach towards the nest and circling around it within a diameter of 1.5 m, (ii) try to enter a nest by darting, i.e. a dwarf male swims very fast directly into the nest. When darting into the nest, we noted (iii) whether dwarf males show mouthing behaviour and/or (iv) successfully spawn or not.

Results

BEHAVIOUR AND TIME BUDGETS OF NEST AND DWARF MALES IN THE FIELD

In the field survey performed in 1998, dwarf males fed for more than 20% of their time, whereas nest males hardly ever fed ($N = 16$ nest males, 15 dwarf males, Mann–Whitney U -test, $U = 0$, $P < 0.001$; Fig. 2). In contrast, nest males exhibited courtship behaviour, which was not shown by dwarf males (U -Test, $U = 0$, $P < 0.001$); the latter only interacted with females inside the shell during parasitic spawning. As expected, territorial males showed much more aggression than dwarf males (U -Test, $U = 1$, $P < 0.001$). The latter only displayed against other dwarf males and very rarely against small fish of other species, whereas nest males defended their territory against both, conspecific males (dwarf males and large intruders) and other fish species (predators and other shell breeders). Spawning was observed by only three territorial males during these focal watches. Males of both types were 'inactive' for about 65% of their time, which did not differ between them (U -Test, $U = 110$, $P = 0.692$). Among the behaviours summarized in the cate-

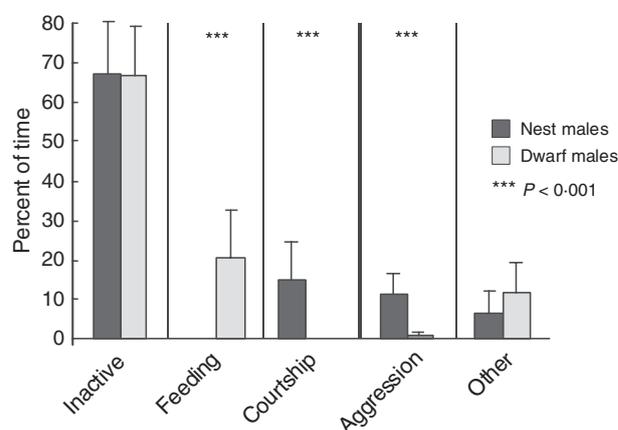


Fig. 2. Time budgets of nest males and dwarf males observed in the field (mean percentages of time and standard deviations, spent per behavioural category).

gory 'other' in Fig. 2, 'fleeing' was significantly more often shown by dwarf males than by nest males (U -test, $U = 48$, $P < 0.001$; data not shown).

BODY RESERVES AND TESTES

Field data collected in 1995 revealed that nest males had a significantly higher GFCF than dwarf males (T -test, $t = 5.436$, d.f. = 78, $P < 0.001$, Fig. 3a). In contrast, dwarf males

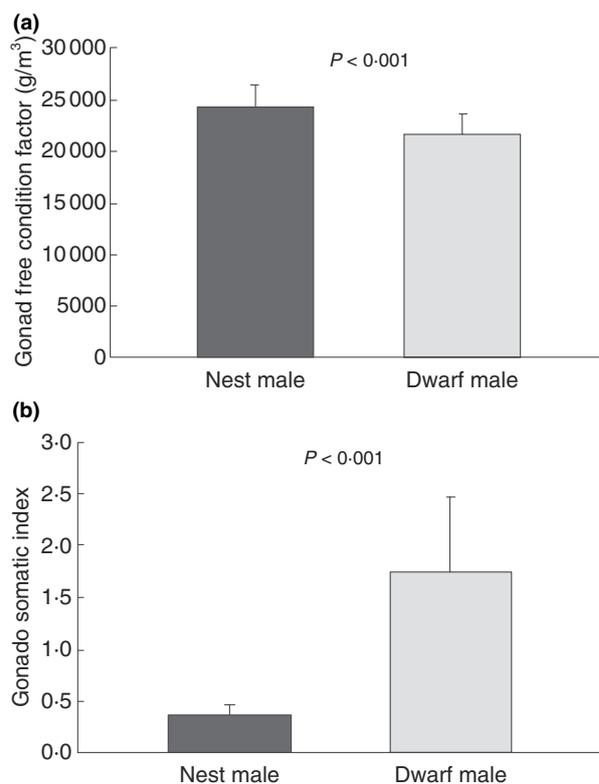


Fig. 3. Gonad free condition factors as a measure of body reserves (means and standard deviations). (a) Gonad free condition factor (g m^{-3}) (b) Gonado-somatic index.

Table 1. Analysis of covariance of log testes mass on male tactic, with the covariate log soma mass before and after the removal of the interaction term

| | Full model | | | | Reduced model | | | |
|------------------------|------------|-------------|----------|----------|---------------|-------------|----------|----------|
| | d.f. | Mean square | <i>F</i> | <i>P</i> | d.f. | Mean square | <i>F</i> | <i>P</i> |
| Model | 3 | 5.948 | 221.22 | 0.000 | 2 | 8.922 | 336.124 | 0.000 |
| Tactic | 1 | 0.002 | 0.093 | 0.762 | 1 | 0.047 | 1.78 | 0.186 |
| Log soma mass | 1 | 0.134 | 4.970 | 0.029 | 1 | 0.288 | 10.842 | 0.002 |
| Tactic × Log Soma mass | 1 | 0.000 | 0.015 | 0.901 | | | | |
| Error | 76 | 0.027 | | | 77 | 0.027 | | |

showed a significantly higher GSI than nest males (mean ± sd, nest males: $0.355 \pm 0.118\%$, dwarf males: $1.735 \pm 0.723\%$; *T*-test, $t = -10.178$, d.f. = 78, $P < 0.001$, Fig. 3b), which might suggest that they invest relatively more in gonads than nest males do. However, an analysis of covariance showed that the interaction term of male tactic × log soma mass did not influence log gonad mass significantly, and therefore we removed it from the model following Tomkins & Simmons (2002; see Table 1 for results of the full and reduced models). This analysis revealed no significant influence of male tactic on log gonad mass (Table 1). The slopes of testis allometry did not differ significantly between the two male tactics, i.e. they were homogenous. Within both male types, the allometric exponents were less than 0.5, showing that smaller males had relatively larger testes, although this was only significant within dwarf males (see Table 2).

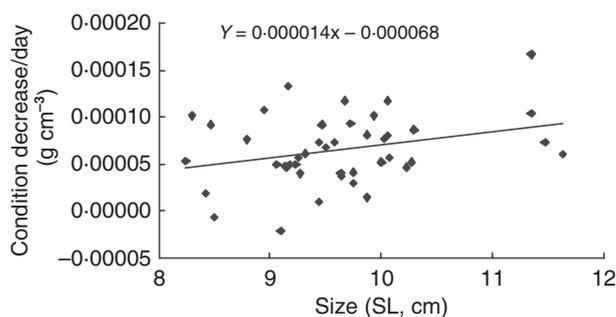
LIMITS TO REPRODUCTION

Condition decrease of nest males by fasting

In the field experiment performed in 1997, the decline in body condition correlated positively with body size, although this relationship was weak (Fig. 4, Pearson correlation analysis, $r = 0.301$, $N = 43$, $P = 0.049$). The average condition decrease per day was $\Delta C_D = 0.0000659 \text{ g cm}^{-3}$. The average minimum and maximum body conditions over three size classes of nest males were $C_{\max} = 0.025748 \text{ g cm}^{-3}$, and $C_{\min} = 0.019665 \text{ g cm}^{-3}$, respectively. Assuming that maximum and minimum condition of nest males reflects their condition close to the start and end of the nest holding period, respectively, the estimate for the mean condition decrease during one nest holding period ($= C_{\max} - C_{\min}$) $\Delta C_N = 0.00679 \text{ g cm}^{-3}$. Thus, with a mean condition decrease of $\Delta C_D = 0.0000659 \text{ g cm}^{-3}$ per day as found in the field experiment, males that loose $\Delta C_N = 0.006083 \text{ g cm}^{-3}$

Table 2. The relationship between $\log_{10}(\text{GWT})$ and $\log_{10}(\text{Soma WT})$ for nest and dwarf males

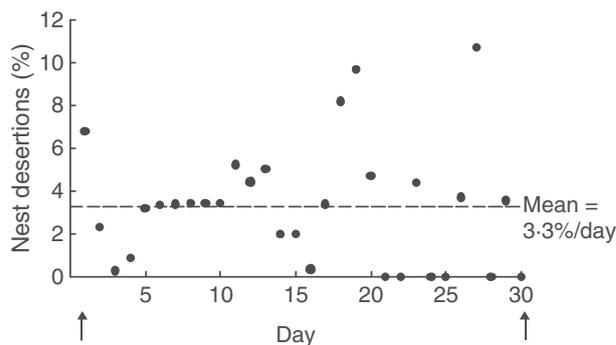
| Male type | Slope | Intercept | <i>r</i> | <i>P</i> | <i>N</i> |
|-------------|-------|-----------|----------|----------|----------|
| Nest males | 0.379 | 0.352 | 0.254 | 0.183 | 29 |
| Dwarf males | 0.424 | -0.152 | 0.376 | 0.007 | 51 |
| Total | 0.584 | -0.585 | 0.947 | 0.0001 | 80 |

**Fig. 4.** Condition decrease of nest males per day (g cm^{-3}) due to opportunity costs in a field experiment, in relation to male body size.

during territory maintenance could hold a territory for $\Delta C_N / \Delta C_D = 103$ days, if food restriction would be their only energetic limitation (i.e. without investment in reproduction).

Nest holding period

In 29 nests sampled in the field during an entire lunar cycle in 2003, the mean percentage of nest males that abandoned their nest was 3.3% per day. The variation was between 0 and 11% desertions per day and the average nest holding period was 33 days. Fig. 5 shows the percentage of nest males abandoning their nest on each day during the monitoring period. Note that this estimation is not biased by possible differences in frequency of nest desertion that might exist in various stages of the lunar cycle, because the monitoring period covered an entire lunar cycle.

**Fig. 5.** Percentage of nest males that abandoned their nest each day during an entire lunar cycle ($N = 16$ –29 nests monitored per day). Arrows indicate full moon.

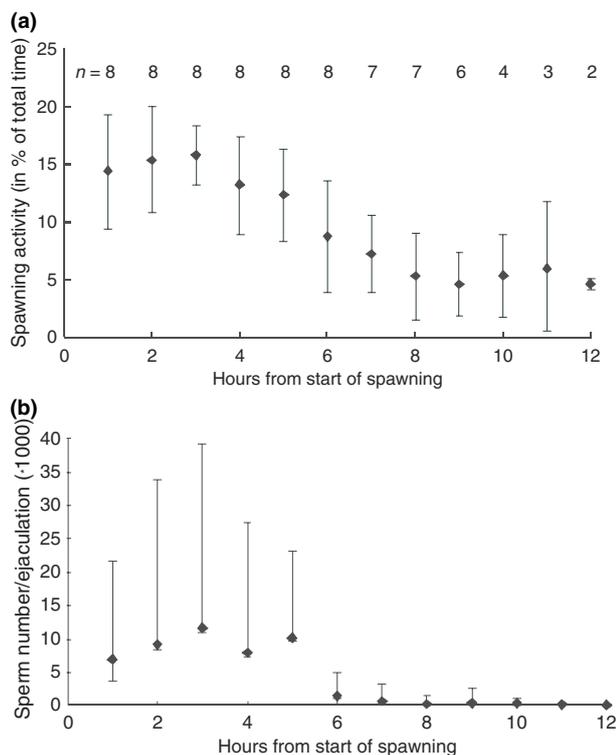


Fig. 6. (a) Spawning activity over time (% of time the territorial male spent with ejaculations during spawning; arithmetic means and standard deviations). (b) Sperm numbers per ejaculation over spawning time (medians, 1st and 3rd quartiles).

Ejaculation rate and spawning duration of nest males

In the laboratory experiment performed in 2001, spawning took on average 9.31 ± 2.15 h (mean \pm SD, $N = 8$, range: 5.5–12 h). The frequency of ejaculations decreased with time (Fig. 6a). The number of sperm released per ejaculate was similar during the first 5 h, before it dropped sharply (Fig. 6b). In the field, spawning took on average 6.88 ± 1.88 h (mean \pm SD, $N = 29$ spawnings at 10 nests, range: 2.16–10.28 h).

Mating access of dwarf males

In the focal dwarf male watches performed in the field in 2005, 26 of 35 observed dwarf males tried to approach the nest during the observation period, and 14 (40%) darted towards the nest, on average 1.57 ± 2.71 times per 42.8 min observation (mean \pm SD). This means that dwarf males darted towards the nest only 0.88 ($0.4 \times 1.57 \times 60$ min/42.8 min) times per hour, or 10.5 times per 12 h daylight period, while they are in the nesting area and actively trying to reproduce. Mouthing behaviour by dwarf males was shown only twice during these observations. Given that dwarf males were observed for a total period of 25 h, we estimate that they show this behaviour on average slightly less than once per 12 h daylight period. No spawning of focal dwarf males occurred during these observations, and dwarf males approaching nests were always immediately chased away at the moment the nest owner returned to his nest.

Discussion

Our data show that the reproductive investment differs substantially between the two male morphs of *L. callipterus*. Behavioural time budgets in the field revealed that both, nest and dwarf males were active for about one third of their time. Nest males invested a lot in courtship behaviour, which was never displayed by dwarf males. In contrast, dwarf males fed for about 20% of the time during their reproductively active period, while bourgeois males largely starved during their entire nest holding periods. Dwarf males exhibited significantly less aggression than nest males. Aggressive behaviour was shown to raise the routine metabolic rate about four-fold in a closely related cichlid (*Neolamprologus pulcher*; Grantner & Taborsky 1998), so apparently nest males bear substantial behavioural energy costs compared to dwarf males, independent of the spawning process itself. Also in the European wrasse *Symphodus ocellatus*, with four types of male alternative reproductive behaviour, satellites never participate in nest building, courtship, direct brood care or interspecific defence (Taborsky, Hudde & Wirtz 1987), even though they cooperate with nest males in defence against other reproductive parasites. This resembles the patterns in other fish taxa like sunfishes (Dominey 1980; Gross 1982) and the Azorean rock-pool blenny (Oliveira *et al.* 2002).

Nest males showed a higher gonad free condition factor (GFCF) than dwarf males, which indicates their greater body reserves. Apparently, nest males need to store reserves for defending and maintaining a territory, as during their territory holding period they cannot leave the nest to feed. Therefore nest males acquire resources for reproduction in advance and use stored energy for reproduction, which is characteristic for 'capital breeders' (Houston *et al.* 2007). The amount of stored resources determines the nest holding period of bourgeois males, which was found to correlate positively with male size (Sato 1994).

Dwarf males had a nearly five times higher gonado-somatic index (1.73%) than nest males (0.36%; see also Sato *et al.* 2004; Schütz *et al.* 2006), which seems to suggest that they invest relatively more in gonads than nest males do. The slopes of testis allometry did not differ significantly between the two male tactics, and were considerably smaller than those of all 23 fish species from 11 families listed by Stoltz, Neff & Olden (2005). This suggests that in *L. callipterus* males, small body size is strongly compensated by high investment in testes, which renders relatively large testes in small individuals, regardless of their reproductive tactic. Interestingly, despite the highly significant difference in GSI between nest and dwarf males, our ANCOVA analysis revealed no significant effect of tactic on testes size, but only a significant body size effect. Nest and dwarf males may compensate with higher gonadal investment for small body size for different reasons, however. For nest males, the crucial limit might be the enormous number of ejaculations (>200) required to fertilize a clutch of one female. For dwarf males, it is probably the intense sperm competition with nest males, which affects virtually 100% of their fertilization attempts.

In addition to the risk of sperm competition, another requirement should affect energy allocation of dwarf males. A fat body (i.e. high condition factor) may be disadvantageous when trying to enter a shell to wriggle past a spawning female (Sato *et al.* 2004). Therefore, dwarf males appear to behave optimally by using resources acquired for reproduction straight away after uptake, instead of using stored energy, which is typical for 'income breeders'. Capital and income breeding are the ends of a continuum, and some species mix the two modes (Stearns 1992). Poeciliid fishes show the full spectrum from capital breeders such as guppies (*Poecilia*) and swordtails (*Xiphophorus*), to income breeders such as the least killifish, *Heterandria Formosa* (Stearns 1992). Also in mammals, there might be a continuum from large species often performing as capital breeders, to small species rather acting as income breeders (Sandell 1989; Festa-Bianchet, Gaillard & Jorgenson 1998; Gould, Sussman & Sauther 2003). Most insects, such as butterflies, are essentially 'capital breeders', because nutrients acquired during the larval stage are stored and subsequently used for egg production during adulthood (Bergstrom & Wiklund 2002). So far, the concepts of capital and income breeding have been mainly used to discriminate between different tactics of resource use between species (Festa-Bianchet, Gaillard & Jorgenson 1998; Poizat, Rosecchi & Crivelli 1999; Boyd 2000; Gregory 2006; Ely *et al.* 2007), but a few studies have shown that this distinction is also useful in the intraspecific context. For example, most snakes are capital breeders (Bonnet *et al.* 1999), but reproducing female vipers may combine energy from 'capital' and 'income' to maximize their litter sizes in the face of fluctuating levels of prey abundance (Lourdais *et al.* 2003). Depending on food availability, the lizard *C. versicolor* adopts a strategy of capital breeding for production of the first clutch of their season, switching to income breeding later in the season when food becomes more abundant (Shanbhag 2003). We argue that capital and income breeding are also very useful concepts to discriminate between tactics within a species and within one sex.

Also the physiological limitations in reproduction appear to differ between nest and dwarf male *L. callipterus*. For nest males, the decrease in somatic condition with increasing time of holding a territory apparently limits their reproductive period. Our condition decrease experiment suggested that nest males could hold a territory for an average period of 103 days, if they were only food limited and had no additional costs of maintaining a territory and reproducing. However, the observed average nest holding period was only 33 days, which suggests that the energetic costs of territory maintenance and reproduction exceeded the opportunity costs entailed by restricted feeding more than two-fold. Sato (1994) found that in a northern population, larger males had longer territory holding periods than smaller males. In our field cage experiment, large males showed a higher condition decrease per day than small males, which was probably caused by the fact that all males, regardless of size, had the same limited space for feeding (i.e. 1 m², corresponding to the natural territory size), which affected small males less severely

than large males. However, large males can accumulate more reserves before founding a territory and they may use energy more efficiently than small males during reproduction, in other words they are more efficient capital breeders. When nest males abandon their territory they roam about outside the nesting area to feed, mostly in conspecific shoals (own obs.). The age distribution of nest owners indicates that multiple nesting periods are possible (Ripmeester 2004), but because of time limitations in our field season we were unable to determine interval lengths between two nesting periods of the same male.

Sperm shortage is another limitation for nest male reproduction. In our lab experiments spawning activity of *L. callipterus* nest males began to decrease after 3 h and dropped sharply after 5 h, even though the spawning of a clutch lasted much longer. *L. callipterus* females lay eggs one by one, so that each egg requires a separate ejaculation (Bachar 2002). Nest males may not be able to anticipate the duration of egg laying by the female. They can only control the number of sperm per ejaculation, but not the number of ejaculations required, which depends on the number of eggs laid and is hence under female control. Therefore, males may run out of sperm during a spawning, which may be more severe even with intense sperm competition in a natural setting.

In contrast, dwarf males appear to be limited primarily by the difficulty to enter a shell and wriggle past a spawning female. Nest males defend their nests very effectively, and the success of dwarf males largely depends on the temporary absence of large males (Sato *et al.* 2004). Combining Sato *et al.*'s (2004) and our results of nest male removal experiments during spawning in the field, in 42.0% of all cases (150 of 357) a dwarf male subsequently entered the nest. In 113 cases the mating behaviour of the dwarf male could be identified: in 71.7% ($N = 81$) dwarf males tried to wriggle into a shell or showed a variation of wriggling behaviour, and in 28.3% ($N = 32$) they showed mouthing behaviour similar to the spawning behaviour of nest males. Compared to these observations, in undisturbed situations, we observed mouthing and successful intrusions into a shell by wriggling each only twice in about 25 h of focal dwarf male observations (see also Sato *et al.* 2004). The comparison of undisturbed observations with experimental removal periods strongly suggests that dwarf males are ready to spawn when they stay near nests, but that they are usually prevented from entering shells or fertilizing eggs by the respective nest owners. Sato *et al.* (2004) found that wriggling was most likely successful when the respective dwarf male was small, and when small females were spawning in relatively large shells. The largest dwarf males may be unable to wriggle past a spawning female, because they never adopted wriggling but only performed mouthing and sperm release similar to medium sized sneaker males (Sato *et al.* 2004).

Our study showed that nest males differ from dwarf males in several behavioural, morphological, and physiological traits concerning reproductive investment and limitations in reproduction. We conclude that nest males usually bear much higher costs than dwarf males, and that nest males conform

to the pattern of 'capital breeders', whereas dwarf males are typical 'income breeders'. We should like to stress that capital breeding may not be the default for bourgeois male tactics in general. When nutritional resources contained in a reproductive territory suffice for the owner's energy maintenance, for example, bourgeois males may be selected to perform as income breeders. Likewise, parasitic males may be selected to accumulate reserves and act as capital breeders, for instance when performing a sit-and-wait tactic at or within bourgeois males' territories. This is indeed a rare behaviour performed by *L. callipterus* dwarf males (Sato *et al.* 2004), and its rarity might relate to the opposing selection pressure to keep their bodies small and slender to enable them to enter a shell during spawning. In *L. callipterus* the reproductive limitations of alternative male types diverge extremely due to their very different spawning performance, which illustrates the effects of disruptive selection in a species with alternative reproductive tactics at the levels of body size, behaviour, somatic and gonadic morphology, and physiology.

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