

## Male alternative reproductive behaviours in a Mediterranean wrasse, *Symphodus ocellatus*: Evidence from otoliths for multiple life-history pathways

Suzanne H. Alonzo,<sup>1\*</sup> Michael Taborsky<sup>2</sup> and Peter Wirtz<sup>3</sup>

<sup>1</sup>Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, USA, <sup>2</sup>Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV), Savoyenstrasse 1A, 1160 Vienna, Austria and <sup>3</sup>Centro de Ciências Biológicas e Geológicas, Universidade da Madeira, Largo do Colégio, 9000 Funchal, Madeira, Portugal

---

### ABSTRACT

Although alternative reproductive behaviours have been studied extensively, it has only been possible in a few cases to document the underlying life-history pathways and factors that determine their expression. In *Symphodus ocellatus*, a Mediterranean wrasse, males adopt a variety of behaviours. Within a season, they may invest in territory defence, nest building and broodcare (nesting males); join nesting males in their defence against reproductive parasites, but also participate in spawning (satellites); parasitize nesting males' spawns (sneakers); or refrain from reproduction (non-reproductives). To examine the life-history patterns of these alternatives, we observed individual males during a reproductive season and categorized their behaviour as sneakers, satellites, nesting males or non-reproductives. We then used their otoliths to estimate age and growth patterns. Males are sneakers, satellites or non-reproductives in their first reproductive season, while they behave as satellites or nesting males when 2 years old. Differences in early growth and behaviour suggest three alternative pathways: switching between reproductive seasons from being non-reproductive directly to nesting, changing from satellite to nesting behaviour between seasons, or from sneaking to adopting satellite behaviour. The adoption of a behaviour is apparently related to growth before reproduction in the first year of life. The existence of four age-dependent alternative behaviours within three separate life-history pathways indicates that we need to determine the life-history pathways that occur before we can infer the underlying mechanisms allowing the stable co-existence of alternative reproductive behaviours in a given species.

*Keywords:* alternative reproductive strategies, bourgeois and parasitic males, life-history pathways, ontogeny.

---

\* Address all correspondence to Suzanne H. Alonzo, Department of Environmental Studies, University of California Santa Cruz, Santa Cruz, CA 95064, USA. e-mail: shalonzo@cats.ucsc.edu  
Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

## INTRODUCTION

There is empirical evidence for alternative reproductive behaviours in many taxa, with a variety of mechanisms being evoked to explain the existence of such variation (Levene, 1953; Gadgil, 1972; Dawkins, 1980; Rubenstein, 1980; Cooper and Kaplan, 1982; Gross, 1982, 1984, 1991, 1996; Waltz, 1982; Austad, 1984; Dominey, 1984; Kaplan and Cooper, 1984; Caro and Bateson, 1986; Moore, 1991; Taborsky, 1994, 1997, 1998; Sinervo and Lively, 1996; Henson and Warner, 1997). Although alternative reproductive behaviours have attracted extensive empirical and theoretical attention, in most cases we know very little about the life-history pathways of the alternatives (for reviews, see Gross, 1984, 1996; Taborsky, 1994, 1998). Consequently, we often compare the expected fitness of alternative behaviours to infer the underlying mechanisms maintaining variation in the population. For example, we could compare the reproductive success of territorial and non-territorial males to determine differences in expected fitness associated with each behaviour. However, if we wish to understand the evolution of alternative reproductive behaviours, knowledge of the life-history pathways is essential.

In a Mediterranean wrasse, *Symphodus ocellatus*, observations have indicated that distinct alternative male reproductive behaviours exist (Soljan, 1930; Fiedler, 1964; Warner and Lejeune, 1985; Taborsky *et al.*, 1987). Large, colourful males defend territories, build nests out of algae, court females and care for the eggs until hatching. Other, smaller males in the population hover around active nests and attempt to join the nesting male's spawns by simultaneous, parasitic spawning (Soljan, 1930; Fiedler, 1964; Lejeune, 1985; Taborsky *et al.*, 1987; Taborsky, 1994). These smaller males (sneakers) have mature testes and sperm capable of fertilizing eggs (Warner and Lejeune, 1985). Intermediate-sized males adopt another behaviour. These individuals, commonly called satellites, associate with nesting males and chase sneaker males from the nests, but parasitize spawns and do not assist in parental care (Taborsky *et al.*, 1987). Some males do not take part in reproduction throughout an entire reproductive season (Taborsky *et al.*, 1987; Taborsky, 1994).

Although Soljan (1930) speculated from growth marks on scales that nesting and parasitic males might represent alternative life-history pathways, the exact life history of *S. ocellatus* male alternative reproductive behaviours is unknown. Switching between nesting and parasitic behaviour has never been observed within a season, but could conceivably occur between reproductive seasons. Nesting and parasitic male standard lengths are significantly different (Taborsky *et al.*, 1987). This pattern might suggest a size-dependent switch between parasitic and nesting behaviour. However, some adult males do not take part in reproduction throughout the entire season, which suggests that future nesting males may invest in growth instead of reproduction in their first year (Taborsky *et al.*, 1987; Taborsky, 1994).

In principle, two basic life-history patterns may exist: (1) Individuals may switch between behaviour types as they grow older and larger. (2) Alternatively, nest building and parasitic behaviour could represent two distinct life histories. If individuals simply show an ontogenetic change in behaviour, male behaviour types should not differ in early growth rates because nesting males simply represent older individuals within a single growth trajectory. However, if separate pathways exist, growth patterns may be distinctly different between behaviour types. For example, individuals destined to be nesting males may show high early growth rates (e.g. Gross, 1982; Taborsky, 1994, 1998). To study the pattern of expression of these alternatives, we examined the age and growth patterns of known *S. ocellatus* males

using otoliths. The reproductive behaviour of these individually marked males had been observed during the reproductive season prior to their collection.

## METHODS

*Symphodus ocellatus* is a Mediterranean wrasse found on rocky and seagrass substrates in shallow coastal waters (Fiedler, 1964). Estimates of adult densities in our study site range from 0.34 to 0.94 individuals per square metre (Lejeune, 1985; Taborsky *et al.*, 1987). There is no evidence for sex change in this species (Warner and Lejeune, 1985; Bentivegna and Benedetto, 1989). The breeding season lasts for approximately 2 months between May and June (Fiedler, 1964; Voss, 1976; Lejeune, 1985), during which time nesting males are temporarily dichromatic (Voss, 1976; Lejeune, 1985). Spawning occurs in nests built out of algae by the large, territorial males (Fiedler, 1964; Lejeune, 1985). All females examined during the reproductive season have active gonads (Warner and Lejeune, 1985; Taborsky *et al.*, 1987). Most males in all size classes above 40 mm have active testes, but some males in this size range were not involved in reproduction in that particular reproductive season. Dissection of these males revealed highly reduced testes (Taborsky *et al.*, 1987; Taborsky, 1994).

Reproductive behaviour is easily observed along rocky coasts in shallow water (Fiedler, 1964; Voss, 1976). Mating occurs daily from sunrise to sunset (Lejeune, 1985). Individuals live up to 3 years (Warner and Lejeune, 1985). All observations and collections were conducted during 1982 and 1983 on the rocky substrate in front of La Station de Recherches Sous-Marin et Océanographique (STARESO) near Calvi, Corsica, France, in depths of 1–8 m along a stretch of approximately 150 m of shoreline.

During 1982 and 1983, a total of 359 individuals were caught throughout the study area at the beginning of the reproductive season and individually marked for the duration of a reproductive season using subcutaneous injections of alcian blue (Thresher and Gronell, 1978; Lejeune, 1985). Marked individuals were then observed whenever encountered throughout the reproductive season ( $n = 297$  individuals). Males could be classified by their behaviour as sneakers, satellites, non-reproductive or nesting males. The latter are easily recognized by their colouration and nesting behaviour. Males classified as sneakers or satellites were observed during the reproductive season to be involved in parasitic spawns at nests. Satellite behaviour can be distinguished from that of sneakers by the satellite male's submissive behaviour towards the nesting male and aggression towards sneaker males (Taborsky *et al.*, 1987). Individuals classified as sneakers were never observed behaving as satellites. Males considered to be satellites occasionally adopted parasitic spawning without adopting the typical aggressive behaviour of a satellite. Non-reproductive males were never seen to be involved in reproduction. Unfortunately, following individuals between years was not possible because alcian blue marks do not usually last between reproductive seasons. Only one individually marked male was observed in both 1982 and 1983. For more details on the reproductive biology of this species and observation methods, see Taborsky *et al.* (1987).

### *Otolith preparation*

At the end of the two reproductive seasons, 110 marked individuals were recaptured, 80 of which were euthanized using MS-222 and preserved in ethanol. Their saggital otoliths

were removed and prepared following a standard procedure. The otoliths were embedded in resin, mounted on slides and ground, allowing the core of the otolith to be exposed. The otoliths were then placed under a microscope and photographed at a standard magnification ( $100\times$ ). A photograph of a  $1\text{ mm}^2$  grid was also taken for calibration. Black and white photographs were printed at a standard size ( $12.7\times 17.8\text{ cm}$ ) and measurements were made from the photographs. A standard measure was exposed with the photographs to determine that the enlargement of the negative was consistent across photo prints. A comparison of measurements from photographs and directly from slides showed such measurements to be consistent between both sources.

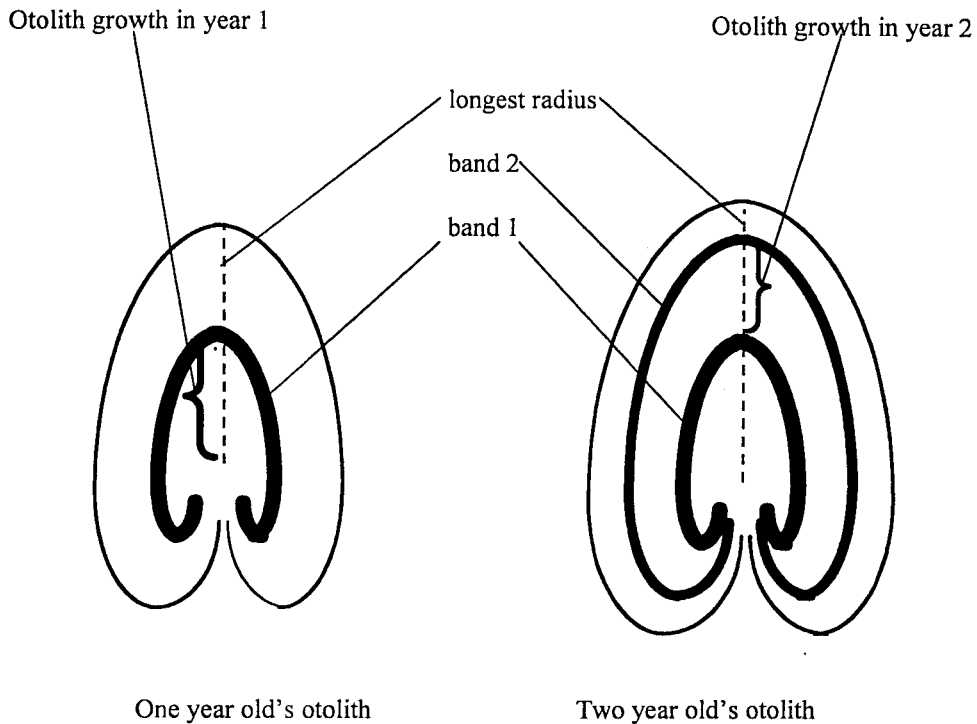
### *Measurements*

First, the number of dark bands was determined for each otolith. This measure indicates the number of winters the fish has survived and is, therefore, an indicator of age (Bagenal, 1974). Otolith growth is commonly used as an indicator of somatic growth (Bagenal, 1974; Campana and Neilson, 1985). All measurements of otolith distance were made along the longest radius from the centre of the otolith (see Fig. 1). Callipers (accurate to 0.1 mm) were used to measure the distance to the first winter band from the centre of the otolith and the width of the first winter band on the photographs. The distance from the core to the distal end of the first winter band was used to estimate growth in the first year. For individuals with two dark bands, we measured the distance between these bands and the width of the second winter band. The distance from the first winter band to the distal edge of the second winter band was used to estimate growth in the second year. The distance from the last band to the edge of the otolith was also measured. These measurements were all taken by one investigator and were made 'blind', that is, without knowledge of the sex or behaviour of the individual fish.

### *Analyses*

We first made comparisons between age cohorts for all otolith measurements to test for between-year effects on growth that might confound comparisons between individuals born in different years. If the assumptions of normality and equal variances were met, we made comparisons using a parametric analysis of variance (ANOVA) and report the associated *F*-statistic. Variables were first tested for significant deviations from normality using a Kolmogorov-Smirnov test (Zar, 1996), and the assumption of equal variances was examined using the Levene Median test (Snedecor and Cochran, 1989). If a variable deviated significantly from normality or equal variance, we conducted a Kruskal-Wallis non-parametric ANOVA on ranks and report the associated *H*-statistic.

We determined the age of individuals by the number of dark bands present. Individuals were classified by their sex, age and behaviour type. We tested whether adopting a specific male behaviour was independent of age using a chi-square test with a Yates correction. We used a chi-squared test, although our data do not conform to the standard rule of thumb that all expected frequencies be equal to or greater than 5 because  $\chi^2$  tests are generally resilient to small samples (Cochran, 1954; Roscoe and Byers, 1971; Koehler and Larntz, 1980; Snedecor and Cochran, 1989; Zar, 1996). However, expected values are always greater than 3. We also compared all relevant variables between 1-year-old and 2-year-old females using a two-sample *t*-test. Females do not show different reproductive behaviour types. Significant differences between 1- and 2-year-old females would therefore indicate a con-



**Fig. 1.** Otolith measurements, showing the first year and second year growth in brackets.

founding effect of age on otolith measurements. Comparisons between all sex, age and behaviour groups were made using a one-way ANOVA. We then examined all reasonable life-history pathways using multiple comparison contrasts with a sequential Bonferroni correction (Holm, 1979; Rice, 1989; Levin, 1997). Comparisons were also made between all groups on all otolith variables (growth in first year, growth in second year and the distance from band 2 to the edge of the otolith).

## RESULTS

### *Comparison between age cohorts*

There were three age cohorts: individuals that were 2 years old in 1982 ( $n = 20$ ), individuals that were 1 year old in 1982 or 2 years old in 1983 ( $n = 38$ ), and individuals that were 1 year old in 1983 ( $n = 21$ ). Only one 3-year-old individual was found. This female was excluded from all analyses. Comparisons were made between the three age cohorts to check for between-year differences in otolith growth. Significant differences were found between age cohorts for both measures (width of band 1:  $H = 6.766$ , d.f. = 2,  $P = 0.034$ ; distance to band 1:  $F = 3.994$ , d.f. = 2,  $P = 0.022$ ). However, because these differences were in opposite directions, total growth in the first year (distance to band 1 plus the width of band 1) did not differ significantly between age cohorts ( $H = 3.236$ , d.f. = 2,  $P = 0.198$ ). This measure, therefore, was used for all future comparisons between behaviour types. No significant

**Table 1.** Age frequencies for each behaviour type

|                   | 1 year | 2 years |
|-------------------|--------|---------|
| Females           | 15     | 11      |
| Sneakers          | 9      | 0       |
| Satellites        | 8      | 11      |
| Non-reproductives | 6      | 1       |
| Nesting males     | 0      | 18      |

Note:  $\chi^2 = 31.66$ , d.f. = 4,  $P < 0.001$ .

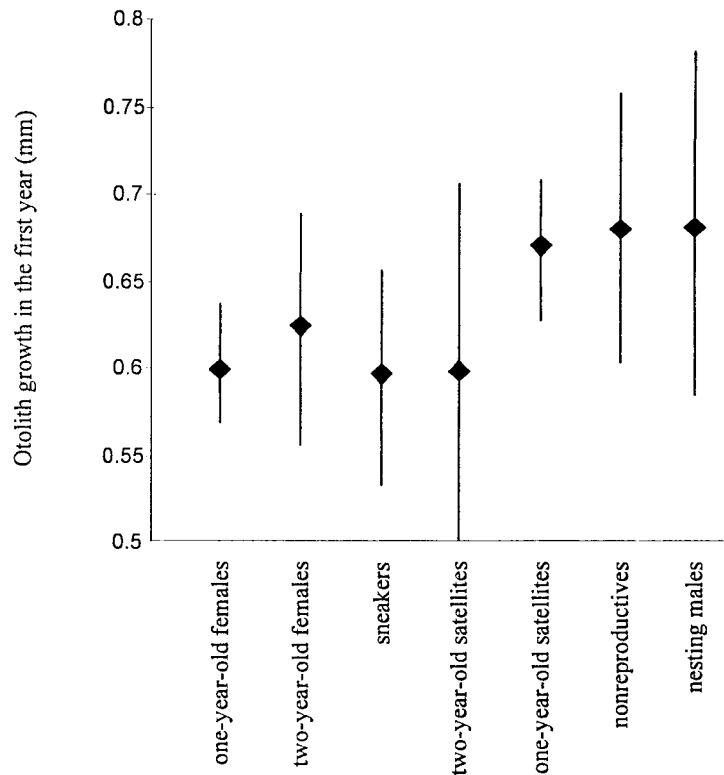
differences were found between the 1982 and 1983 age cohorts for any otolith measurements in 2-year-old individuals ( $1 - \beta > 0.971$  with  $\alpha = 0.05$  for all otolith measurements). We also found no significant differences between 1-year-old and 2-year-old females in any variable, suggesting that age itself had no significant effect on otolith measurements ( $1 - \beta > 0.999$  with  $\alpha = 0.05$  for all measures).

#### *Comparison between behaviour types*

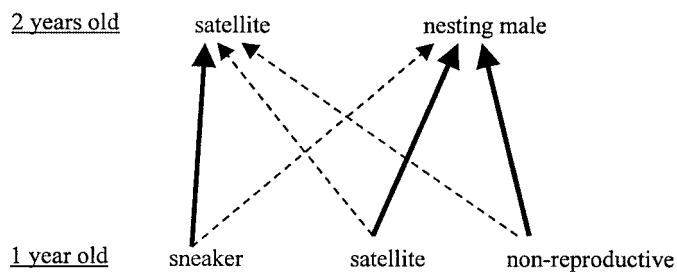
Individuals had been classified as females ( $n = 28$ ), sneakers ( $n = 9$ ), satellites ( $n = 19$ ), non-reproductive males ( $n = 7$ ) or nesting males ( $n = 18$ ). Comparing the frequency of 1- and 2-year-olds in each behaviour group, we found that behaviour type was not independent of age in the population sampled (Table 1). All sneakers were 1 year old and all territorial males were 2 years old. Comparison of otolith growth in the first year suggested significant differences between groups ( $F = 3.129$ ,  $P = 0.009$ ,  $n = 78$ ) (Fig. 2). Given that basically three behaviours are adopted by 1-year-old males (sneaker, satellite or non-reproductive) and two behaviours are adopted by 2-year-old males (satellite or nesting), six possible life-history patterns exist. Therefore, six contrasts were made between male behaviour types that could represent the same life history. Only one contrast showed significant differences between means. This contrast indicated that nesting males, 1-year-old satellites and non-reproductive males had significantly greater growth in their first year than sneakers and 2-year-old satellites ( $F = 12.34$ ,  $P < 0.0001$ ). We found no significant differences between behaviour types for any other otolith measurements. Therefore, the only observed differences in otolith growth occurred in the first year prior to reproduction (growth in year 2:  $F = 0.1154$ ,  $P = 0.8913$ ,  $n = 40$ , with  $\alpha = 0.05$  and  $1 - \beta = 0.0664$ ; distance to edge:  $F = 0.6162$ ,  $P = 0.5455$ ,  $n = 40$ , with  $\alpha = 0.05$  and  $1 - \beta = 0.1450$ ). Although alcian blue marks do not usually last between reproductive seasons and most of the marked individuals were collected at the end of each season, a single male was observed in 1982 and 1983. This male was classified as a satellite male in both years and was one of the smallest satellites in 1982 and one of the largest in 1983. Unfortunately, no other individuals were observed in multiple reproductive seasons.

## DISCUSSION

Our results suggest the existence of three life-history pathways (Fig. 3). Since both non-reproductives and 1-year-old satellites have early growth similar to nesting males, there are two possible pathways to nesting behaviour (Fig. 3). Non-reproductive males apparently



**Fig. 2.** Otolith growth in the first year varies between age and behaviour groups (mean  $\pm$  standard deviation). Sneaker males and 1-year-old satellites have significantly lower early growth than non-reproductive males, 2-year old satellites and nesting males.



**Fig. 3.** Theoretically possible life-history pathways (dashed lines) of male alternative reproductive behaviours in *S. ocellatus*, and those supported by otolith growth data (bold lines).

delay reproduction in their first year and behave as nesting males in their second year, while individuals that are satellites in their first year also become nesting males. Sneakers become satellites in their second year (Fig. 3). It is important to realize that these early growth differences are not the result of differences in reproductive behaviour because they exist prior to the first reproductive season. It is also notable that the life-history patterns

observed are quite different from the expected dichotomy between either ontogenetic or separate life histories of parasitic and territorial alternatives. Instead, we have one pathway that includes parasitic and territorial behaviour, another that involves two types of parasitic behaviour and a third involving delayed reproduction. Clearly, the patterns are more complex than we tend to consider theoretically.

Soljan (1930) also compared the growth patterns of *S. ocellatus* male behaviour types. It is difficult to compare our results directly with those of Soljan, since we used otoliths while he used scales, he had very small sample sizes, and we distinguished between satellites and sneakers while he did not. However, he also argued that non-reproductive males and nesting males comprise one life-history pathway while sneakers and satellites comprise another. In addition, we found that satellites can also become nesting males. By distinguishing between satellites and sneakers, we found this additional life-history pattern not detected by Soljan.

It has been suggested that the origin of alternative male life-history pathways can be viewed at three different levels: determination, plasticity and selection (Taborsky, 1998). Our results are not suited to judge the determination of reproductive tactics in *S. ocellatus* (i.e. whether or to what extent these are genetically fixed or environmentally induced) or evaluate the relative benefits of different trajectories with respect to lifetime reproductive fitness (i.e. if different pathways result in the same or unequal Darwinian fitnesses). Our results do, however, reveal that a degree of plasticity exists because males switch behaviours between years. Although we cannot eliminate completely the possibility that these alternative life-history pathways are genetically determined, it is more probable that early growth differences caused by settlement date or environmental conditions influence the size at maturity, and thus the adoption of one or the other lifetime strategy. Obviously, growth differences between males have the potential to determine life-history pathways in *S. ocellatus*, as also demonstrated in Atlantic and Coho salmon (Dalley *et al.*, 1983; Metcalfe *et al.*, 1989; Gross, 1991).

Our level of otolith analyses cannot discriminate between differences in growth rate and length of the growth period. If some individuals were born and settled early in the season, they could grow more slowly but still have the same otolith growth and size as another individual that grew faster for a shorter period of time. In *S. ocellatus*, males that reproduce lose weight during the reproductive season while non-reproductive males increase their weight (Taborsky, 1994). As a result, small individuals reproducing as 1-year-olds may not grow large enough to compete as nesting males in their second year. This would explain the existence of the year-one-sneaker-to-year-two-satellite pathway inferred from the similarity in pre-reproductive growth of these two classes. Alternatively, larger and fast-growing individuals may be able to start their first year as satellites and still grow enough to be nesting males in their second year. Individuals that are large at the beginning of their first reproductive season may adopt still another alternative. Large males that grow less quickly may refrain from reproduction as 1-year-olds to speed growth (Taborsky, 1994, 1998) and become nesting males in the next season. For this tactic to make sense, delaying reproduction must yield overall higher or equal fitness as behaving as sneakers or satellites in their first year and foregoing nesting behaviour in their second. Given the overriding importance of early reproduction (Stearns, 1992), this is a serious cost to bear. An alternative possibility is that, for some other reason, these males are unable to reproduce.

Our results also do not allow us to discriminate between the four potential mechanisms underlying a size-based choice of life-history trajectories: (1) absolute size (i.e. based on a mechanism involving size thresholds), (2) relative size (i.e. based on evaluation of success



probabilities including frequency dependence), (3) speed of growth (i.e. based on individual or environmental quality) and (4) environmental cues (such as daylight or temperature during early ontogeny). These mechanisms are clearly not mutually exclusive.

Although there are discrete behaviours and an indication of separate life histories, early growth distributions do overlap, and there may in fact be a continuum in which early growth influences the probability of adopting certain behaviours (for example, see the documented case in which a small satellite remained in the satellite role in the subsequent year). It is possible that further life-history pathways occur that we did not detect. The sample sizes of some groups were small and the power of some of the contrasts were low. Similarly, mortality may mean that some pathways are less probable than others.

In conclusion, the life history of *S. ocellatus* includes the typical dichotomy between territorial and parasitic behaviours (Taborsky, 1994, 1997) and a third option – not reproducing at all. However, the actual life-history pathways include a parasitic pathway (sneaker to satellite), a territorial life history (non-reproductive to nesting) and a third that combines both types of behaviour (satellite to nesting). Furthermore, age-dependent alternatives and within-age alternatives occur within one species. Thus, simple dichotomies do not hold true at the level of the life history. Researchers have previously compared the reproductive success of parasitic and nesting males to determine if these two behaviours represent separate life histories with equal fitness (Warner and Lejeune, 1985; Taborsky *et al.*, 1987). It is clear, however, that the life-history pathways of *S. ocellatus* are much more complex. To determine if these pathways have equal fitnesses, we need to determine the fitness of each behaviour at each age as well as behaviour-dependent survival and growth. For example, it makes no sense to examine satellite mating success as a whole. Instead, we must compare the expected lifetime reproductive success of 1-year-old satellites with sneakers and non-reproductive males. This demonstrates that one needs to know the life-history pathways that occur before comparing the fitness of alternative behaviours to infer the underlying mechanism allowing their co-existence.

#### ACKNOWLEDGEMENTS

We are grateful to Barbara Taborsky for assistance in the field and to Dr Schultz for preparing and photographing the otoliths. We also thank John Endler, Marc Mangel, Roger Nisbet and Robert Warner for their helpful comments, which greatly improved the manuscript. The field and laboratory work of M.T. and P.W. were supported by the Deutsche Forschungsgemeinschaft and the Max-Planck-Gesellschaft. S.H.A. was supported by NSF grant IBN97-00948 and an American Association of University Women American Dissertation Fellowship.

#### REFERENCES

- Austad, S.N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. *Am. Zool.*, **24**: 309–319.
- Bagenal, T.B. 1974. *The Ageing of Fish*. Old Woking: Unwin Press.
- Bentivegna, F. and Benedetto, F. 1989. Gonochorism and seasonal variation in the gonads of the labrid *Symphodus ocellatus*. *J. Fish Biol.*, **34**: 343–348.
- Campana, S.E. and Neilson, J.D. 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.*, **42**: 1014–1032.
- Caro, T.M. and Bateson, P. 1986. Organization and ontogeny of alternative tactics. *Anim. Behav.*, **34**: 1483–1499.

- Cochran, W.G. 1954. Some methods for strengthening the common  $\chi^2$  tests. *Biometrics*, **20**: 191–195.
- Cooper, W.S. and Kaplan, R.H. 1982. Adaptive coin-flipping: A decision-theoretic examination of natural selection for random individual variation. *J. Theor. Biol.*, **94**: 135–151.
- Dalley, D.L., Andrews, C.W. and Green, R.H. 1983. Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. *Can. J. Fish. Aquat. Sci.*, **40**: 647–652.
- Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? In *Sociobiology: Beyond Nature's Nurture* (G.W. Barlow and J. Silverberg, eds), pp. 331–367. Boulder, CO: Westview Press.
- Dominey, W.J. 1984. Alternative mating tactics and evolutionarily stable strategies. *Am. Zool.*, **24**: 385–396.
- Fiedler, K. 1964. Verhaltensstudien an Lippfischen der Gattung *Crenilabrus* (Labridae, Perciformes). *Z. Tierpsych.*, **21**: 521–591.
- Gadgil, M. 1972. Male dimorphism as a consequence of sexual selection. *Am. Nat.*, **106**: 574–580.
- Gross, M.R. 1982. Sneakers, satellites, and parental males: Polymorphic mating strategies in North American sunfishes. *Z. Tierpsych.*, **60**: 1–26.
- Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In *Fish Reproduction: Strategies and Tactics* (G.W. Pott and R.J. Wootton, eds), pp. 55–75. London: Academic Press.
- Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology*, **72**: 1180–1186.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: Diversity within the sexes. *TREE*, **11**: 92–98.
- Henson, S.A. and Warner, R.R. 1997. Male and female alternative reproductive behaviors in fishes: A new approach using intersexual dynamics. *Ann. Rev. Ecol. Syst.*, **28**: 571–592.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.*, **6**: 65–70.
- Kaplan, R.H. and Cooper, W.S. 1984. The evolution of developmental plasticity in reproductive characteristics: An application of the adaptive coin-flipping principle. *Am. Nat.*, **123**: 393–410.
- Koehler, K.J. and Larntz, K. 1980. An empirical investigation of goodness-of-fit statistics for sparse multinomials. *J. Am. Stat. Assoc.*, **75**: 336–344.
- Lejeune, P. 1985. Etude écoéthologique des comportements reproducteur et sociaux des Labridae méditerranéens des genres *Symphodus* (Rafinesque 1810) et *Coris* (Lacepede 1802). *Cah. Ethol. App.*, **5**: 1–208.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. *Am. Nat.*, **87**: 331–333.
- Levin, J.R. 1997. Overcoming feelings of powerlessness in 'aging' researchers: A primer on statistical power in analysis of variance designs. *Psychology and Aging*, **12**: 84–106.
- Metcalfe, N.B., Huntingford, F.A., Graham, W.D. and Thorpe, J.E.. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proc. R. Soc. Lond. B*, **236**: 7–19.
- Moore, M.C. 1991. Application of organization-activation theory to alternative male reproductive strategies: A review. *Horm. Behav.*, **25**: 154–179.
- Rice, W.R. 1989. Analyzing tables of statistical test. *Evolution*, **43**: 223–225.
- Roscoe, J.T. and Byers, J.A.. 1971. Sample size restraints commonly imposed on the  $\chi^2$  statistic. *J. Am. Stat. Assoc.*, **66**: 755–759.
- Rubenstein, D.I. 1980. On the evolution of alternative mating strategies. In *Limits to Action: The Allocation of Individual Behaviour* (J.E.R. Staddon, ed.), pp. 65–100. London: Academic Press.
- Sinervo, B. and Lively, C.M. 1996. The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, **380**: 240–243.
- Snedecor, G.W. and Cochran, W.G. 1989. *Statistical Methods*. Ames, IA: University of Iowa Press.
- Soljan, T. 1930. Die Fortpflanzung und das Wachstum von *Crenilabrus ocellatus* Forsk. einem Lippfisch des Mittelmeeres. *Z. Wiss. Zool.*, **137**: 150–174.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

- Taborsky, M. 1994. Sneakers, satellites and helpers: Parasitic and cooperative behavior in fish reproduction. *Adv. Study Behav.*, **21**: 1–100.
- Taborsky, M. 1997. Bourgeois and parasitic tactics: Do we need collective, functional terms for alternative reproductive behaviours? *Behav. Ecol. Sociobiol.*, **41**: 361–362.
- Taborsky, M. 1998. Sperm competition in fish: Bourgeois males and parasitic spawning. *TREE*, **13**: 222–227.
- Taborsky, M., Hudde, B. and Wirtz, P. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. *Behaviour*, **102**: 82–118.
- Thresher, R.E. and Gronell, A.M. 1978. Subcutaneous tagging of small reef fishes. *Copeia*, **2**: 352–353.
- Voss, J. 1976. Apropos de quelques poissons de la Mediterranee: *Symphodus (Crenilabrus) ocellatus* Forskal, 1775. *Rev. Franc. Aquariol.*, **3**: 96–98.
- Waltz, E.C. 1982. Alternative mating tactics and the law of diminishing returns: The satellite threshold model. *Behav. Ecol. Sociobiol.*, **10**: 75–83.
- Warner, R.R. and Lejeune, P. 1985. Sex change limited by parental care: A test using four Mediterranean labrid fishes, genus *Symphodus*. *Mar. Biol.*, **87**: 89–99.
- Zar, J.H. 1996. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.

