# When to parasitize? A dynamic optimization model of reproductive strategies in a cooperative breeder

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## Abstract

We consider a cooperatively breeding group and find the optimal pattern of reproductive parasitism by a subordinate helper as a function of its body size, and hence the share of reproduction obtained by the subordinate. We develop the model for the social system of the cooperatively breeding cichlid fish *Neolamprologus pulcher* but the general framework is also applicable to other cooperative systems. In addition to behaving cooperatively by sharing tasks, sexually mature male cichlid helpers may directly parasitize the reproduction of dominant breeders in the group. We investigate the relative influence of life history and behavioural variables including growth, parasitism capacity, future reproductive fitness benefits and costs, relatedness and expulsion risk on the optimal reproductive strategy of subordinates. In a detailed analysis of the parameter space we show that a male helper should base its decision to parasitize primarily on an increase in expulsion risk resulting from reproductive parasitism (punishment), intra-group relatedness and the parasitism capacity. If expulsion risk is high then helpers should not parasitize reproduction at medium body size but should parasitize either when small or large.
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## 1. Introduction

Social systems with complex levels of behavioural interactions, such as cooperative breeding groups, may provide various options for group members to increase their fitness. Subordinate cooperative breeders may share in reproduction, either as concessions (Clutton-Brock, 1998) or because of the dominants' incomplete control of reproduction (Reeve et al., 1998). Subordinates have developed a variety of alternative reproductive strategies (see Rohwer and Freeman, 1989; Taborsky, 1994; Reeve and Keller, 2001 for reviews).

The cichlid *Neolamprologus pulcher* is a cooperative breeder endemic to Lake Tanganyika. Social groups consist of a pair of breeders and immature and mature helpers of both sexes, and large helpers may successfully reproduce within the family (Taborsky, 1984, 1985; von Siemens, 1990; Dierkes et al., 1999). Although helpers of all body sizes may contribute to the indirect reproductive success of breeders, simultaneous parasitic spawning (SPS, Taborsky, 1994) by male helpers causes direct fitness costs to the territorial male and therefore has been viewed as reproductive parasitism (Taborsky, 1997). Female helpers may split off part of the territory (harem foundation) or pair up with the breeding male and expel the former female breeder (own obs.; P. Dierkes, pers. comm.).

In this paper we consider whether a male helper should indulge in reproductive parasitism. The fitness costs and benefits of parasitism may change as the helper grows and current alternatives need to be weighed against future fitness expectations. This may be achieved by dynamic programming (Bellman, 1957; extended by e.g. Howard, 1960; Shapiro, 1979), which has been used in behavioural ecology to predict

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sequences of behaviour that maximize lifetime fitness (McNamara and Houston, 1986; Houston et al., 1988; Mangel and Clark, 1988; Ludwig and Rowe, 1990; Clark, 1993; Houston and McNamara, 1999; Clark and Mangel, 2000; for a review see McNamara et al., 2001). It has been applied by Lucas et al. (1997) to show that future fitness effects, relatedness and mortality influence delayed dispersal in cooperatively breeding dwarf mongooses, and by Yerkes and Koops (1999) to predict reproductive parasitism in non-cooperatively breeding female redhead ducks. Our approach is novel in that we consider reproductive parasitism by brood care helpers within a consistent life history framework that includes complex interactions between kin over time.

## 2. The system

The cichlid *Neolamprologus pulcher* (described as *N. pulcher* and *N. brichardi*[2]) occurs along the shore of Lake Tanganyika. Data used in this model were derived from the northernmost morph studied near Magara, Burundi. There, two social alternatives have been documented (Taborsky and Limberger, 1981): (i) breeding adults maintain territories and their offspring stay there beyond sexual maturity ($\gtrsim 35$ mm standard length) and act as helpers; (ii) expelled former helpers live in permanent aggregations in the vicinity of territories. These fish do not show territorial behaviour or participate in reproduction, and they stay in the aggregation until they are large enough to be able to take over and defend a territory of their own (i.e. for males at about 60 mm SL; Taborsky, 1984).

Among the fish on a territory there is a status-dependent specialization either in direct brood care, territory maintenance (substrate cleaning, digging) or territory defence (Taborsky and Limberger, 1981; Taborsky et al., 1986). Body size determines social status, helping ability and behaviour, growth, mortality risk and fecundity (Taborsky, 1985, 1994). Therefore it is the relevant state variable of a helper in this model. The breeding pair attacks large helpers aggressively (Taborsky, 1985) and the latter react with intensive submissive behaviour. This raises the helpers' energetic costs and may slow down growth (Taborsky, 1984; Grantner and Taborsky, 1998; Taborsky and Grantner, 1998).

In groups with helpers, breeders are able to reduce their workload (Balshine et al., 2001) and spend more time feeding and therefore they can invest additional

energy in offspring production (Taborsky, 1984). *N. pulcher* reproduces in clefts between rocks or under stones. The spawning female attaches batches of eggs to the ceiling of a shelter and alternates with the male partner in visiting the breeding shelter and releasing gametes (Skubic, unpubl. data). Male helpers may parasitize the breeders' reproduction, darting towards the clutch and releasing sperm during this spawning. This parasitism gives the helper a benefit in terms of the immediate production of offspring, but it also has costs in terms of future reproductive success. One cost is a reduction in growth. Other costs arise from an increased probability of being evicted from the territory as a consequence of parasitism. An evicted helper has a reduced probability of survival. Furthermore, its absence from the territory reduces the reproductive success of the adult pair and hence may reduce the helper's inclusive fitness.

## 3. The model

In *N. pulcher* the timing of reproduction of male helpers depends entirely on the reproductive behaviour of the breeders, which produce several broods ($B_1, B_2, \ldots, B_i, \ldots, B_j$) during the ontogeny of a helper (see Fig. 1). Therefore we consider the time between two broods as a reproductive routine. We assume that the brood cycles last 60 days on average (range: 12–120 days; Taborsky, 1982). We divide each cycle into six discrete 10-day time intervals to reflect a realistic change of the helper's state over time. Time $t = 0$ corresponds to the start of the brood cycle, time $t = 1$ to the start of the next 10-day interval, and so on. Time $t = T$ $(= 6)$ corresponds to the end of the brood cycle and the start of a new cycle. At the beginning of the interval $t = 0$, the helper decides whether to parasitize the brood (action $P$) or not to parasitize (action $\bar{P}$). The action chosen determines the probability that the helper is expelled from the territory by the breeders. If the helper is not expelled it may nevertheless die at this time. Provided that the helper is neither expelled nor dies at time $t = 0$, it helps until time $t = 1$. At times $t = 1$ up to $t = T - 1$ the helper makes no reproductive decision and if it is neither expelled nor dies, it helps until time $t + 1$.

### 3.1. The state

The state of a helper, $x$, is its body size. Length rather than weight is the relevant variable in this system because small differences in length directly determine the outcome of aggressive interactions (Taborsky, 1984). We assume that male helpers are able to compete for and maintain a territory of their own when $x \geqslant 60$ mm standard length (SL). This body length at the helper's independence is referred to as the "critical length" $x_c$.

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[2] 1974 separated as species (Poll, 1974, 1986), there is morphological evidence (S. Balshine, E. Skubic, P. Dierkes & M. Taborsky, unpubl. data) that *N. pulcher* (southernmost morph) and *N. brichardi* (northernmost morph) should be regarded as subspecies or populations of one species (Grantner and Taborsky, 1998). Therefore we refer to the species name *N. pulcher* throughout this study.
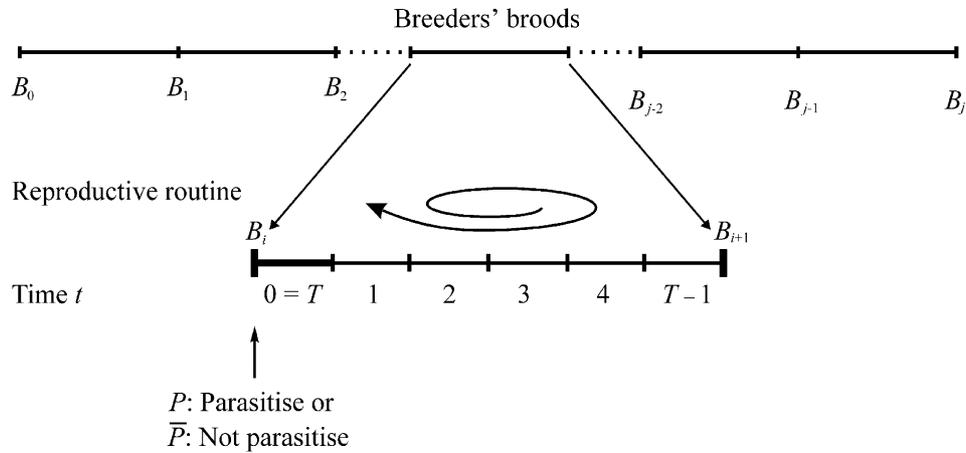
Fig. 1. Schematic description of the time-scale of the reproductive routine. Brood cycles are assumed to last for 2 months on average. $B_i = i$th brood of the breeders ($i = \{0,1,\ldots,j\}$). $B_0$: first helper generation is born. $t = 0 = T$: beginning of one particular brood cycle; $0 < t < T$: time periods within the cycle. Each period is assumed to last 10 days. The arrow indicates the cyclic, iterative procedure of the dynamic programming.

We consider sequential behavioural decisions of a male helper during its growth to this critical size. Thus the optimization problem has a final state rather than a final time.

If the male helper has size $x$ at time $t$ its size at time $t + 1$ is $x + g$. Here the deterministic growth increment $g$ can potentially depend on (i) $x$, (ii) whether the helper is in the aggregation or on a territory (Taborsky, 1984), (iii) its behaviour and (iv) the time in the cycle if it is helping. Specifically, if the focal male is in the aggregation then the growth increment is $g = g_A(x)$. If the male helper does not parasitize at the beginning of the current cycle the growth increment $g = g_{\bar{P}}(x)$ depends on size but not on time in the cycle. *N. pulcher* helpers may suffer a growth cost when parasitizing (i) because of the necessity to show more submissive behaviour, which is energetically expensive (Grantner and Taborsky, 1998; Taborsky and Grantner, 1998), and (ii) since they need to produce gametes, which has been shown to be costly in fish (Nakatsuru and Kramer, 1982). We denote the growth increment of a helper that parasitized at the beginning of the current cycle by $g = g_P(x, t)$. This growth increment depends on both size and time in the cycle. Computations are based on the assumption that the effects of parasitism on growth do not persist beyond the first 10-day period in a cycle. Thus we assume that $g_P(x, 0) < g_{\bar{P}}(x)$ and that $g_P(x, t) = g_{\bar{P}}(x)$ for $t = 1, \ldots, T-1$.

Fish growth is often found to follow a sigmoidal function of time (DeAngelis and Coutant, 1982; Lundberg and Smith, 1994; Nagoshi and Yanagisawa, 1997). Parameterized versions of the original Verhulst logistic growth model such as the logistic, generic, Von Bertalanffy, Gompertz, Richards or Blumberg growth curves may be applied (see Tsoularis and Wallace (2002) for a comparison of growth models). Growth data of

*N. pulcher* helpers are best represented by Blumberg's hyperlogistic function. We assume that

$$\frac{\mathrm{d}x}{\mathrm{d}t} = bx^{\alpha}\left[1 - \left(\frac{x}{x_{\infty}}\right)\right]^{\gamma}.$$

The relation between $\alpha$ and $\gamma$ determines the location of the maximum growth rate (the inflection point) of the function. $x_{\infty}$ is the known species-specific asymptotic size ($x_{\infty} = 65.0\,\mathrm{mm}$) and $\mathrm{d}x/\mathrm{d}t \to 0$ as $x \to x_{\infty}$. We make the discrete approximation that the growth increment over one time interval is

$$g = \frac{\mathrm{d}x}{\mathrm{d}t}n, \tag{1}$$

where $n$ is the interval length in days (here $n = 10$).

To estimate the parameters $b$, $\alpha$ and $\gamma$ we performed nonlinear regressions (Kleinbaum and Kupper, 1978; McCallum and Dixon, 1990) for the growth of non-parasitizing helpers $g_{\bar{P}}(x)$ and for the growth of aggregation members $g_A(x)$. In both of these cases $g(x)$ is a concave function of body length $x$ (see Fig. 2a). The maxima of the resulting growth functions are $g_{\bar{P}}(x)_{max} = 1.5895\,\mathrm{mm}/10\,\mathrm{d}$ at $x = 19.8\,\mathrm{mm}$ SL and $g_A(x)_{max} = 1.4926\,\mathrm{mm}/10\,\mathrm{d}$ at $x = 14.7\,\mathrm{mm}$ SL, respectively (see Fig. 2a; for statistical details see Table 1). These functions satisfy $g_A(x) > g_{\bar{P}}(x)$ for $x > 30.6\,\mathrm{mm}$ SL so that growth of large fish is faster in the aggregation.

### 3.2. Survival

Helpers receive protection, which is important particularly until they reach a length of 40–45 mm SL, at which their main predator, *Lepidiolamprologus elongatus* (Boulenger, 1898; Poll, 1986) can hardly prey on them any more (Taborsky, 1984). Predation is the main cause of mortality in cichlids (e.g. Nagoshi, 1987) and is
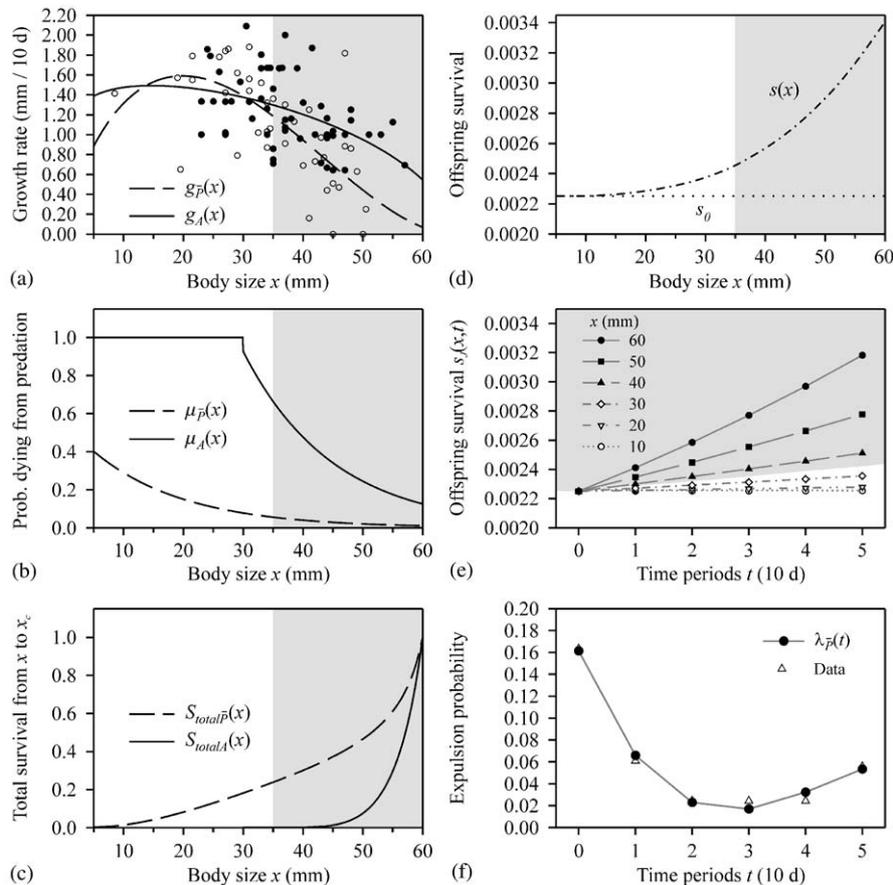
Fig. 2. Functions for the basic assumptions of the model (see also Table 1). (a)–(d) Size-dependent functions plotted over the whole range of a helper's body cize $x$ (5–60 mm); (e)–(f) functions depending on time $t$ of the brood cycle. $\bar{P}$ =no parasitism (also dashed black lines); $A$ = aggregation (also solid black lines). Note that the option to parasitize is only available at sizes of $x \geqslant 35.0$ mm (shaded areas), and at time $t = 0$. (a) Growth rates (mm/10 d) of helpers (open circles) and aggregation members (solid circles). Helpers: field data ($N = 6$, M. Taborsky, unpubl.) and aquarium data ($N = 35$, Taborsky, 1984) were combined because they did not differ significantly ($U$-test; size range for which data from both samples were available (SR): 41.0–50.5 mm SL, $N_1 = 5$, $N_2 = 10$, $u = 21$, $p = 0.679$). Aggregation members: two sets of aquarium data ($N = 18$, Taborsky, 1984; $N = 40$, Skubic, unpubl.) were combined because of no significant differences ($U$-test; SR: 24.5–42.0 mm SL, $N_1 = 18$, $N_2 = 20$, $u = 137$, $p = 0.217$). (b) Probability of dying during one time period (10 d) for helpers and aggregation members. (c) Total survival probability of aggregation members from $x$ to $x_c$; for comparison, the total survival probability of helpers is also plotted. (d) Survival of offspring due to breeders' ($s_0$) and breeders' plus focal helper's defence ($s(x)$). (e) Proportion of young produced at the beginning of a brood cycle that survive to independence $s_J(x,t)$. (f) Expulsion probability of helpers during the brood cycle; Data = calculated expulsion probabilities per period in the brood cycle from data of Taborsky (1985).

viewed as the key factor changing intra-group related-ness and thereby causing a switch from kin advantages being responsible for helping behaviour to a reciprocal association between helpers and breeders in *N. pulcher* (Taborsky, 1985). We define a size-dependent mortality risk due to predation $\mu(x)$, which represents the probability of being caught by a predator (e.g. *L. elongatus*, Mastacembellidae and several species of Siluroidea catfish) within the current time interval. We assume an exponentially decreasing function of mortality with length

$$\mu(x) = m e^{-ax}, \qquad (2)$$

where $m$ and $a$ are positive constants with $0 < a \leqslant 1$. Consequently, $1 - \mu(x)$ is increasing with length and represents the probability of surviving one time period. We do not have mortality data of helpers from the field

and therefore we make assumptions based on length class distributions from Taborsky (1984) to estimate the parameters $m$ and $a$ for Eq. (2). We assume that predation causes a mortality of helpers $\mu_H(x)$ of 40% within the first period after birth (5 mm SL), which declines to 10% at 30 mm SL (shortly before maturity) and to 5% at maturity (35 mm SL), and becomes zero at 45 mm SL (sudden decrease of predation). For aggregation members we assume that mortality $\mu_A(x)$ is 100% for small fish (no survival during one time period of 10 d), 90% at 30 mm SL, 50% at 45 mm SL, 10% at 50 mm SL and reduces to zero at $x_c$. We estimated the parameters $m$ and $a$ by nonlinear regressions (see Fig. 2b; parameter estimates are given in Table 1).

An individual of length $x$ in the aggregation survives an interval with probability $1 - \mu_A(x)$ and its length is then $x + g_A(x)$. Let $S_{totalA}(x)$ be the probability that an

Table 1
Functions, parameters and basic assumptions used in the model

*Functions and parameter values*

| Variable | Definition | Parameters | Estimation |
|---|---|---|---|
| $dx_{\bar{P}}/dt$ | Instantaneous growth rate of helpers (mm/d); function $g_{\bar{P}}(x)$ | $b = 0.0278613$ $\alpha = 0.806957$ $x_{\infty} = 65.0$ mm | Nonlinear regression $r^2 = 0.4437$, $N = 41$, $SE = 0.0394$, $\chi^2 = 0.059$ |
| | | $\gamma = 1.8386$ | |
| $dx_A/dt$ | Instantaneous growth rate in the aggregation (mm/d); function $g_A(x)$ | $b = 0.112834$ $\alpha = 0.154683$ $x_{\infty} = 65.0$ mm | Nonlinear regression $r^2 = 0.1820$, $N = 58$, $SE = 0.0327$, $\chi^2 = 0.059$ |
| | | $\gamma = 0.530532$ | |
| $\mu_H(x)$ | Probability that a helper dies due to predation | $m = 0.5576$ $a = 0.0657$ | Nonlinear regression $r^2 = 0.9858$, $N = 4$ |
| $\mu_A(x)$ | Probability that an aggregation member dies due to predation | $m = 6.81$ $a = 0.0665$ | Nonlinear regression $r^2 = 0.9067$, $N = 4$ |
| $S_{totalA}(x)$ | Survival probability from $x$ to $x_c$ when a helper is expelled at size $x$ | | Backward iteration |
| $\lambda_{\bar{P}}(t)$ | Expulsion probability when helping | $h_1 = 0.16147077$ $h_2 = 0.12708160$ $h_3 = 0.03412191$ $h_4 = 0.00260580$ | Standard curve fitting $r^2 = 0.9893$, $N = 5$, $F = 61.8$, $p = 0.016$ |
| $s_0$ | Offspring survival prob. to independence when breeders care alone | $s_0 = 0.00225$ | See text |
| $s(x)$ | Offspring survival prob. to independence when breeders and helpers care | $d_1 = 2.3383 \times 10^{-9}$ $d_2 = 3.2033$ | Nonlinear regression $r^2 = 0.9624$, $N = 4$ |
| $N_H - N_0$ | Reproductive benefit due to helping (additional breeders' offspring; helper effect) | $N_0 = 58.57$ $N_H = 85.97$ | See text |

*Varied factors*

| Variable | Definition | Basic assumption | Variation range |
|---|---|---|---|
| $g_P(x)$ | Instantaneous growth rate when parasitizing (mm/10 d) | $g_P(x,t)/g_{\bar{P}}(x) = 0.80$ | [0.40, 0.95] |
| $f$ | Relative reproductive benefit due to parasitism (parasitism capacity) | $f = 0.10$ | $0.0 \leqslant f \leqslant 1.0$ |
| $\lambda_P(0)$ | Expulsion probability (punishment) when parasitizing | $\lambda_P(0)/\lambda_{\bar{P}}(0) = 2.0$ | [1.0, 6.0] |
| $R > \theta$ | Expected fitness at size $x \geqslant x_c$ | $\theta = 0.504$ and $R = 0.75$ | $0.25 \leqslant R \leqslant 1.25$ |
| $F = r_{\bar{P}}N_0 s_0 \eta$ | Future fitness without a helper | $F = r_{\bar{P}} \cdot 0.1317825$, $\eta = 1.0$ | $1.0 \leqslant \eta \leqslant 2.0$ |

$x$: body size (mm SL), $t$: 10-day time periods within individual brood cycles (compare Fig. 1). Nonlinear regressions of $dx/dt$ (mm/d) of the Blumberg growth functions $g_P(x)$ and $g_A(x)$ were estimated by setting the asymptotic size of *N. pulcher* adults equal to $x_{\infty} = 65.0$ mm. The goodness of fit of the various functions fitted to data was determined by the variance measure $F$, the standard error of the estimate $SE$ and the $\chi^2$ goodness-of-fit statistic ($\chi^2 = SE^2 \cdot (N_{data\ points} - N_{parameters})$; used criteria: $SE < 0.1$; $\chi^2 < 0.1$;). The given precision of the estimated constants is significant for the shape of the functions. The residuals of the nonlinear regressions and the curve fitting errors were normally distributed (Kolmogorov–Smirnov-Normality Test). Adjusted regression coefficients are presented throughout. $\eta$: variation factor of future fitness $F$; for explanations of other variables see text. The sample size used in the nonlinear regressions of $\mu_H(x)$ and $\mu_A(x)$ result from assumptions on mortality estimates (see text).

individual of length $x$ in the aggregation survives until the critical length $x_c$ is reached. Then

$$S_{totalA}(x) = [1 - \mu_A(x)] \cdot S_{totalA}[x + g_A(x)], \qquad (3)$$

where $S_{totalA}[x + g_A(x)]$ denotes the total survival probability to $x_c$ after growth. Hence $S_{totalA}(x)$ can be found

from backwards iteration using the terminal condition $S_{totalA}(x_c) = 1$ (see Fig. 2c).

As body length increases, helpers participate more intensely in defence against competitors and predators. Their defence effort is significantly higher than that of breeders (Taborsky and Limberger, 1981). To quantify the increased survival of offspring as a result of the

presence of the focal male helper we assume that its presence has an effect only during the cycle in which the offspring are born. This is reasonable because offspring mortality rapidly decreases with size and the defence of the helper is most effective during the first 2 months of life. We assume that a proportion $s_0 = 0.00225$ of the offspring survive to independence (i.e. reach $x_c$) when no helpers are present for this cycle. We assume further that the presence and defence of a male helper during the whole brood cycle increases offspring survival by one-half for a helper of length $x_c$, one-third for a big helper (45–54 mm SL), 8.3% for a small helper (35–44 mm SL; i.e. one-quarter of the value of a big helper) and 0% for a newly hatched fish (5 mm SL). We performed a nonlinear regression assuming that survival in the presence of a helper of length $x$ has the form $s(x) = s_0 + d_1 x^{d_2}$ (see Fig. 2d; for parameters see Table 1). Now suppose that the male helper is present between times 0 and $t$ in a cycle, but not for the remainder of the cycle. Let the male helper have size $x$ at time $t$. Then we assume that the proportion of young produced at the start of the cycle that survive to independence is

$$s_J(x, t) = [s(x)]^{t/T}[s_0]^{(T-t)/T} \tag{4}$$

(see Fig. 2e). This formula ignores size changes of the helper during a cycle, but this seems reasonable because growth of mature helpers during a single cycle is relatively small (mean $\pm$ S.D. $= 12.6 \pm 9.4\%$ of their actual body length, $N = 22$; calculated from Taborsky, 1984 and M. Taborsky, unpubl. data).

### 3.3. Expulsion

Taborsky (1985) showed that *N. pulcher* helpers do not leave their natal territory of their own accord. Hence we assume that staying within a family or living in an aggregation is determined by the probability that helpers are expelled by breeders $\lambda$. Expulsion probability depends strongly on the stage of the brood cycle, $t$. For example, it is 16 times higher on the day of spawning than on the remainder of the breeding cycle. We calculated the expulsion probability of a male helper that does not parasitize at the beginning of the cycle $\lambda_{\bar{P}}(t)$ from data of Taborsky (1985). By a curve fitting analysis we estimated a cubic function

$$\lambda_{\bar{P}}(t) = h_1 - h_2 t + h_3 t^2 - h_4 t^3, \tag{5}$$

where $h_1, \ldots, h_4$ are constants (the values are given in Table 1; see Fig. 2f).

There is evidence that the expulsion probability strongly increases when helpers parasitize (Taborsky, 1985). In reproductive parasitism experiments in the lab, two of three helpers were expelled after they performed SPS, and the third one was restricted to the edge of the territory by the breeders' attacks (Dierkes et al., 1999). In the model, parasitism can only occur at time $t = 0$.

We assume that the expulsion probability of a helper that parasitizes at this time, $\lambda_P(0)$, is greater than the expulsion probability of a helper that does not parasitize, $\lambda_{\bar{P}}(0)$ (see Table 1 for the basic assumption). We also assume that the expulsion probability after the first 10-day interval is independent of behaviour shown at spawning so that $\lambda_P(t) = \lambda_{\bar{P}}(t)$ for $t = 1, \ldots, T - 1$.

### 3.4. Reproduction

In *N. pulcher* helpers we distinguish between three different components of inclusive fitness: offspring related to the helper that are produced by the breeders, offspring produced as a result of reproductive parasitism and offspring produced once the helper has a territory itself. We measure all three in terms of the number of offspring that survive to independence at size $x_c$, multiplied by the respective degrees of relatedness.

### 3.4.1. Indirect fitness benefits

If the behaviour of the helper affects the breeders' reproductive success and the helper is related to the breeders' offspring then we must take into account the effect of kin selection (Hamilton, 1964). This effect is expressed in two ways: the helper's behaviour (i) raises the survival of the current brood and (ii) increases the number of eggs produced by a breeding pair. Let $N_0$ denote the number of eggs produced when there is no helper and let $N_H$ be the number of eggs produced when a helper is present. We estimated egg production by breeders based on the assumption that in the field, *N. pulcher* produce only half the number of eggs that they produce in the lab (this was derived from comparing the numbers of free-swimming fry in both situations [M. Taborsky, unpubl. data], because eggs cannot be directly observed in the field). The number of eggs produced by breeders alone is $N_0 = 58.57$ (in the lab: mean $\pm SD = 117.13 \pm 84.30$, $n = 8$ broods) and the number of eggs produced by breeders that have helpers is $N_H = 85.97$ (in the lab: mean $\pm SD = 171.93 \pm 81.98$, $n = 14$ broods). Thus, the "helper effect" $N_H - N_0$ is 27.4 offspring, i.e. 46.79%, and it is independent of helper length (linear regression: $N = 18$ helpers, $r^2 = 0.0004$, $p = 0.94$, M. Taborsky, unpubl. data).

Let $r_{\bar{P}}$ be the relatedness between the helper and the offspring produced by the breeders when the helper does not parasitize. Then $r_{\bar{P}} = r$ where $r$ is the average relatedness of the helper to the two breeders. Various coefficients of relatedness are possible. For example (i) If the helper is itself an offspring of both breeders, $r = 0.5$; (ii) if either (a) the female breeder has been replaced during the helper's ontogeny, or (b) the male breeder has been replaced, or (c) if the helper resulted from a parasitic spawning, $r = 0.25$; (iii) when both breeders have been replaced since the helper's birth or when the

Table 2
Degrees of relatedness between a male helper and its own as well as the breeding pair's offspring, depending on the continued presence of the helper's parents

| Presence of parents | Relatedness to offspring of breeding pair $r_{\bar{P}}$ | Difference $r_P - r_{\bar{P}}$ | Relatedness to own offspring $r_P$ |
|---|---|---|---|
| Both | 0.50 | 0.25 | 0.75 |
| Mother only | 0.25 | 0.50 | 0.75 |
| Father only | 0.25 | 0.25 | 0.50 |
| None | 0.00 | 0.50 | 0.50 |
| Average $r$ | 0.30 | 0.35 | 0.65 |

Average $r$: average relatedness calculated from field data (for explanations see text).

mother has been replaced and the helper arose from SPS, $r = 0$. Intermediate values of relatedness may occur when one or both breeders are siblings or other relatives of the focal helper. Helpers may either react to some average probable relatedness since they did not respond directly to changes in territory ownership (Taborsky, 1982) or behave as if they knew the actual value of $r$ (Stiver et al., unpubl. data). In our calculations we assume that relatedness does not change over time and use constant measures of average relatedness as well as actual relatedness between the focal helper and breeder's offspring (see Table 2). We estimated the average degree of relatedness between a helper and each of the breeders by $\bar{r} = 2 \times 0.25(1 - p)^k$ (based on Taborsky and Limberger, 1981), where $p = 2/1566$ is the average replacement rate of breeders, and $k$ is the age of the helper. We calculated $k$ from the growth function $g_{\bar{P}}(x)$. A fish of size $x_c = 60$ mm SL will be 973 days old (2.7 years) and after maturity ($x = 35.0$ mm SL, $k = 220$ days) it may expect $\leqslant 13$ consecutive broods of the breeders if it stays in the territory for the entire period and the breeders spawn every 60 days on average. We used the mean of two helpers' ages (maturity: $k = 220$ and biggest *N. pulcher* helper of the northernmost morph found in the field: $x = 56.0$ mm SL, $k = 624$ days).

### 3.4.2. Reproductive parasitism

In the case of reproductive parasitism, the helper's current fitness increment depends on the proportion $f$ of young that are produced by its SPS. This proportion of parasitically fertilized eggs will be called the helper's "parasitism capacity". As a first approximation we assume it to be constant after sexual maturity ($x \gtrsim 35.0$ mm SL) and vary it to determine its influence on the helper's optimal reproductive strategy. The average degree of relatedness between a male helper that parasitizes and its own offspring is taken to be $r_P = 0.5 + 0.5\bar{r}$, since $0.5\bar{r}$ is the estimated average relatedness between the male helper and the female parent.

### 3.4.3. Reproductive success at independence

We assume that after becoming independent at the critical length $x_c$ the male helper obtains a territory with probability $\xi = 0.5$. Assuming a 60-day brood interval and deriving breeder mortality from the probability of breeder disappearance (Taborsky and Limberger, 1981), we infer that a breeder produces 10.83 broods on average. We estimated $\bar{N} = 71.65$ eggs per clutch (mean egg production by breeders alone and breeders with helpers; again half the number that is produced in the lab). Each egg survives to independence with probability $\bar{s} = 0.0026$ (estimated as mean offspring survival with breeders, small helpers and big helpers present). Assuming a coefficient of relatedness of offspring to the former helper of $r = 0.5$, its expected future reproductive success at length $x_c$ is $\theta = r\bar{N}\bar{s} \times 10.83\xi = 0.504$ offspring equivalents.

### 3.5. The optimization criterion

We take as our optimization criterion the maximization of a suitable measure of the focal male's lifetime reproductive success. One possible measure of lifetime success is the sum of the offspring that reach size $x_c$, multiplied by the degree of relatedness to the focal male, produced by (i) the breeders in the natal territory; (ii) SPS by the male as a helper; and (iii) the male after independence. In maximising this quantity the absolute number of (discounted) offspring produced by the breeders is not relevant, only the difference that the male helper's behaviour makes to this number is important. The problem with this measure is that it fails to take account of the different times at which offspring reach independence. In particular, since offspring produced by the focal male after independence are produced later than offspring produced as a result of helping or parasitizing, the discounted value of offspring at independence has some value $R$ where $R > \theta$. An exact determination of $R$ would require specification of the time of production of all offspring (both direct and indirect). Since much of this information is only approximately known from observation, and since the estimate of $\theta$ is uncertain, we take the future reproductive success of the focal male at independence to be $R$ rather than $\theta$ and perform a sensitivity analysis over values of $R$ in the range $0.25 \leqslant R \leqslant 1.25$.

### 3.6. The dynamic programming equations

Before deriving the dynamic programming equations we must first quantify one of the disadvantages of parasitizing the breeders. The probability that the male helper is expelled from the territory is greater if it parasitizes than if it does not (Dierkes et al., 1999). Once the helper is expelled the breeding pair produces less young in future brood cycles. Furthermore, without

protection from a helper these young have a lower chance of survival. The cost of expulsion in terms of its effect on future broods thus depends on the number of future cycles of the breeding pair and how many of these are without a helper. To give an extreme example, suppose that the breeding pair continues to reproduce forever. Then it might be argued that, since the male helper will eventually leave the territory, it will always pay the cost of expulsion, and hence this cost is irrelevant to optimal behaviour. Our approach is to assume that on completion of one brood cycle, the parents start another with probability $\beta$. We then analyse what happens in the limit as $\beta$ tends to 1. This will expose the logic of how expulsion costs should be quantified and will show why the argument of zero expulsion costs is not tenable.

Throughout this section, by the term 'expected future reproductive success of a male helper' we mean the contribution (weighted by relatedness) from the current parental brood, all future broods produced by the breeders, and the helper itself after reaching independence. In quantifying this success we adopt the mathematical convention that the helper is assigned the contribution from the current brood as follows. If it helps for the whole of the brood cycle then the contribution is assigned at its end. If it fails to help for the whole cycle because of expulsion or death, then the contribution is assigned when help ceases. The contribution to the helper's success from the breeders' broods produced after the helper ceases to care is denoted by $F_{total}$. The direct contribution to the helper's success when it reaches independence at size $x_c$ is denoted by $R$. Let $V(x)$ be the expected future reproductive success of the helper given that it is on the territory and has size $x$ at the start of a brood cycle. We now explain the dynamic programming equations satisfied by $V$.

Consider a male helper that does not parasitize at the beginning of a cycle. Suppose it is still on the territory at time $t$ in the cycle and has size $x$ at this time. Then the probability that it is expelled or dies at this time is

$$c_{\bar{P}}(x,t) = \lambda_{\bar{P}}(t) + [1 - \lambda_{\bar{P}}(t)]\mu_H(x). \tag{6}$$

If this occurs then the contribution to its success from the current brood is

$$R_{\bar{P}}(x,t) = r_{\bar{P}} N_H s_J(x,t). \tag{7}$$

Thus averaging over the possibilities that the helper (i) is expelled or dies during a cycle, (ii) is expelled and survives the aggregation phase or (iii) remains tolerated and grows according to (1), its expected future reproductive success is

$$W_{\bar{P}}(x,t) = c_{\bar{P}}(x,t)[R_{\bar{P}}(x,t) + F_{total}] \\ + \lambda_{\bar{P}}(t)S_{totalA}(x)R + [1 - c_{\bar{P}}(x,t)] \\ \times W_{\bar{P}}(x + g_{\bar{P}}(x), t+1). \tag{8}$$

This equation is valid for $t$ between 0 and $T-2$. We can extend it to hold for $t = T-1$ provided we set

$$W_{\bar{P}}(x,T) = R_{\bar{P}}(x,T) + \beta V(x) \\ + (1-\beta)S_{totalA}(x)R \tag{9}$$

to allow for uncertainty of a new brood cycle. Now consider a helper that parasitized at the beginning of a cycle. Suppose that the helper is still on the territory at time $t$ and has size $x$. The probability that it is expelled or dies at this time is

$$c_P(x,t) = \lambda_P(t) + [1 - \lambda_P(t)]\mu_H(x). \tag{10}$$

If it is expelled the contribution to its success from the current brood is

$$R_P(x,t) = [r_P f + r_{\bar{P}}(1-f)]N_H s_J(x,t). \tag{11}$$

Thus its expected future reproductive success is

$$W_P(x,t) = c_P(x,t)[R_P(x,t) + F_{total}] \\ + \lambda_P(t)S_{totalA}(x)R + [1 - c_P(x,t)] \\ \times W_P(x + g_P(x,t), t+1). \tag{12}$$

Again, this equation is valid for $t$ between 1 and $T-1$ provided we set

$$W_P(x,T) = R_P(x,T) + \beta V(x) \\ + (1-\beta)S_{totalA}(x)R. \tag{13}$$

We can complete the loop from cycle end to start with the dynamic programming equation

$$V(x) = \max\{W_{\bar{P}}(x,0), W_P(x,0)\}. \tag{14}$$

Finally, since the helper is expelled if its size reaches $x_c$ (see Appendix for detailed assumptions on the expulsion probability for large helpers) we have

$$W_{\bar{P}}(x,t) = R_{\bar{P}}(x,t) + F_{total} + R \\ \text{for } x \geqslant x_c \text{ and } 0 \leqslant t \leqslant T-1, \tag{15}$$

$$W_P(x,t) = R_P(x,t) + F_{total} + R \\ \text{for } x \geqslant x_c \text{ and } 0 \leqslant t \leqslant T-1. \tag{16}$$

We now transform these equations as follows. Let

$$W_{\bar{P}}^*(x,t) = W_{\bar{P}}(x,t) - F_{total}, \tag{17}$$

$$W_P^*(x,t) = W_P(x,t) - F_{total} \tag{18}$$

and

$$V^*(x) = V(x) - F_{total}/\beta. \tag{19}$$

Then the above equations become

$$W_{\bar{P}}^*(x,t) = c_{\bar{P}}(x,t)R_{\bar{P}}(x,t) + \lambda_{\bar{P}}(t)S_{totalA}(x)R \\ + [1 - c_{\bar{P}}(x,t)]W_{\bar{P}}^*(x + g_{\bar{P}}(x), t+1), \tag{20}$$

$$W_{\bar{P}}^*(x,T) = R_{\bar{P}}(x,T) + \beta V^*(x) \\ + (1-\beta)S_{totalA}(x)R, \tag{21}$$

$$W_P^*(x,t) = c_P(x,t)R_P(x,t) + \lambda_P(t)S_{totalA}(x)R \\ + [1 - c_P(x,t)]W_P^*(x + g_P(x,t), t+1), \tag{22}$$

$$W_P^*(x, T) = R_P(x, T) + \beta V^*(x)$$
$$+ (1 - \beta) S_{totalA}(x) R, \qquad (23)$$

$$W_{\bar{P}}^*(x, t) = R_{\bar{P}}(x, t) + R$$
$$\text{for } x \geqslant x_c \text{ and } 0 \leqslant t \leqslant T - 1, \qquad (24)$$

$$W_P^*(x, t) = R_P(x, t) + R$$
$$\text{for } x \geqslant x_c \text{ and } 0 \leqslant t \leqslant T - 1, \qquad (25)$$

$$V^*(x) = \max\{W_{\bar{P}}^*(x, 0), W_P^*(x, 0)\}$$
$$- F_{total}(1 - \beta)/\beta. \qquad (26)$$

We now turn attention to $F_{total}$. After the helper is expelled or dies the parents go through $\beta/(1 - \beta)$ expected further brood cycles. Thus the mean success per cycle, averaged over all future cycles is

$$F = \frac{(1 - \beta)}{\beta} F_{total}.$$

It follows that Eq. (26) can be rewritten as

$$V^*(x) = \max\{W_{\bar{P}}^*(x, 0), W_P^*(x, 0)\} - F. \qquad (27)$$

We now look at the limit as $\beta$ tends to 1; that is we allow the number of future brood cycles to tend to infinity. As this occurs $(1 - \beta)/\beta$ tends to zero and $F_{total}$ tends to infinity. The product tends to the finite limit $F$. Thus in this limit as $\beta$ tends to 1, the dynamic programming equation (27) makes sense. The presence of the term $F$ shows, however, that future expectations affect the solution and, even in this limit there is a cost of expulsion. We solve Eqs. (20)–(25) plus Eq. (27) in the case that $\beta = 1$. For all calculations we use a discretiza-

tion of $x$ with 0.025 mm SL distances and linear interpolation.

### 3.7. Reproductive success on the territory after helper expulsion

Suppose that after the expulsion of the helper, all future breeding attempts of the breeding pair do not involve any other helper. The reproductive success of the breeders averaged over all future cycles is

$$F = r_{\bar{P}} s_0 N_0. \qquad (28)$$

If the breeding pair gets another helper then this will increase clutch size and offspring survival. If a new male helper parasitizes then this will decrease the relatedness of the focal male to offspring produced in these broods. Thus whether or not $F$ is greater than the above $F$ depends on detailed assumptions. Our approach is to take $F$ given by Eq. (28) as a baseline and perform a sensitivity analysis, varying $F$ about this baseline. The results are robust regarding different values of offspring survival probability to independence, $s_0$.

## 4. Results

We can find the optimal strategy by plotting the fitness functions $W_{\bar{P}}^*(x, 0)$ and $W_P^*(x, 0)$ against size $x$ (Fig. 3). The optimal action is the one with the higher $W$. A general feature of the optimal policy is that there is a critical size $x^*$ above which the male helper should parasitize and below which it should not parasitize
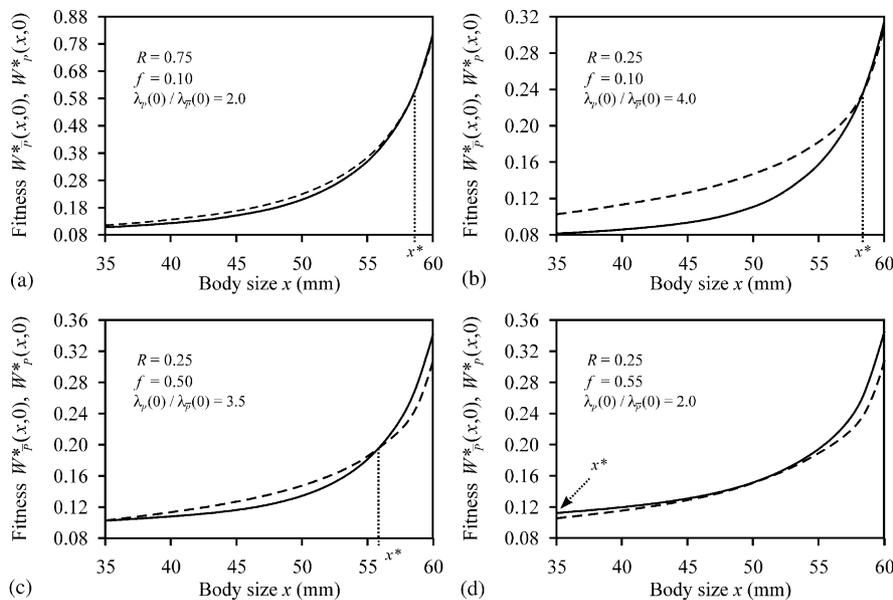


Fig. 3. Fitness functions for the non-reproductive option $W_{\bar{P}}^*(x, 0)$ (dashed lines) and for reproductive parasitism $W_P^*(x, 0)$ (solid lines). The calculations are based on the basic assumptions (see also Table 1) $g_P(x)/g_{\bar{P}}(x) = 0.8$, the male helpers' average degrees of relatedness, ($r_{\bar{P}} = 0.30$, $r_P = 0.65$; Table 2) and $\eta = 1.0$. (a) $\lambda_P(0) = 0.323$; the optimal size to switch to reproductive parasitism $x^* = 58.225$ mm. (b) $\lambda_P(0) = 0.646$; $x^* = 58.35$ mm. (c) $\lambda_P(0) = 0.565$; $x^* = 55.85$ mm. (d) $\lambda_P(0) = 0.323$; $x^* = 35.0$ mm.

(e.g. Fig. 3). Plots of the fitness functions show not only the optimal strategy but also the advantage of selecting the optimal action and so give an indication of the strength of selection. For example when $R$ is low and parasitism strongly increases the probability of being expelled from the territory (high $\lambda_P(t)/\lambda_{\bar{P}}(t)$), the optimal size to start parasitism, $x^*$, stays approximately the same as it is in Fig 3a, but the advantage of not parasitizing becomes much greater for small helpers (Figs. 3b and c). If the parasitism capacity is high and relative expulsion risk is low, reproductive parasitism is optimal from maturity onwards ($x^* = 35$ mm SL) but its relative benefit is low for medium sized helpers (Fig. 3d; there is no intersection between the curves).

The increased probability of expulsion if a male helper parasitizes strongly influences the helper's current reproduction. Especially when the future fitness in a territory of its own, $R$, is high, parasitism should almost never occur if, for example, $\lambda_P(0)/\lambda_{\bar{P}}(0) \geqslant 1.5$ and helpers can fertilize 20% or less of the current clutch (Fig. 4a). If they are able to fertilize about 30% of the clutch, large helpers but also small, recently matured helpers should switch to reproductive parasitism when the expulsion risk is increased by 1.5 ($\lambda_P(0) = 0.242$). Medium sized helpers are predicted to refrain from reproduction and only invest in alloparental care unless they can fertilize more than 50% of the clutch. When the expected future fitness $R$ is low, parasitism becomes more advantageous (Fig. 4b) but remains strongly constrained by the relative expulsion risk.

There may also be a critical lower size above which the male helper should not parasitize and below which it should parasitize (Figs. 4 and 5). This means that as a male grows, it may first be optimal for it to parasitize and then optimal not to parasitize and finally optimal to parasitize. When a male helper successfully fertilizes eggs of the breeders' current clutch it receives an immediate fitness benefit. If the parasitism capacity $f$ is very low only large helpers should switch to reproduction (Fig. 5a). When $f$ increases, small and large helpers should reproduce, but medium sized helpers should refrain from reproduction. The degree of relatedness of helpers to the breeders' offspring has an important influence on the optimal strategy (Fig. 5a). When both parents are still present in the territory helpers should mostly invest in caring for kin. Mainly the presence of a male helper's father should constrain reproductive parasitism. When the father is still present, parasitism should be performed at larger sizes compared to when a non-related male breeder is present. The presence of the mother has only a minor effect on the optimal helper behaviour. For high parasitism capacities ($f \geqslant 0.55$, and basic assumptions for the other variables), parasitizing is always the best strategy when only the mother or none of the genetic parents are present.
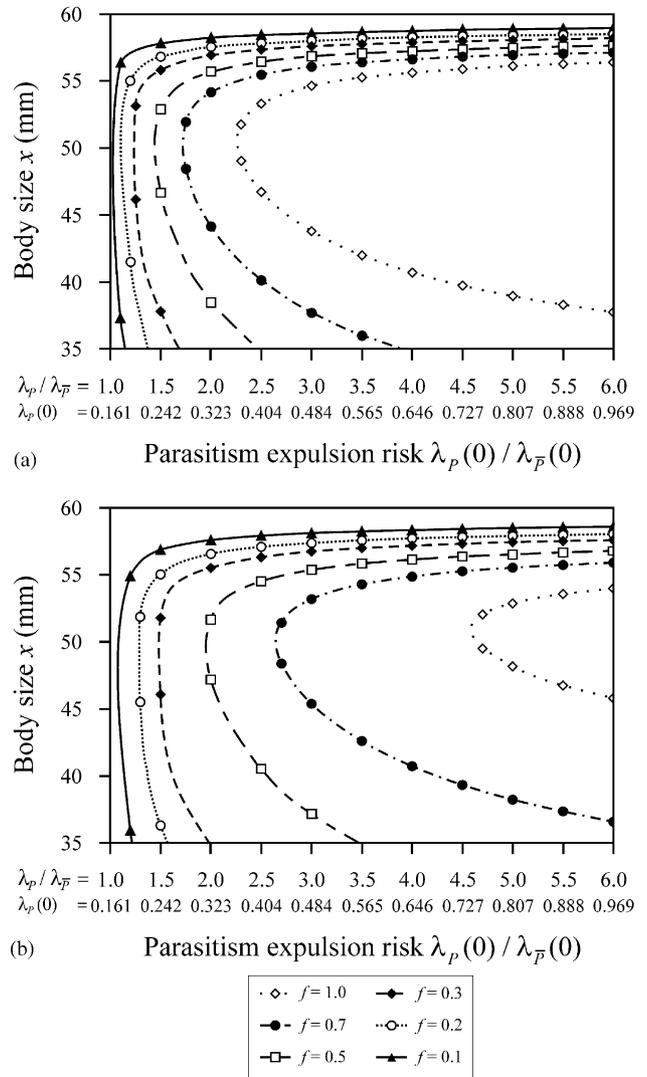


(a)



(b)

Fig. 4. Effect of the relative expulsion probability due to parasitism $\lambda_P(0)/\lambda_{\bar{P}}(0)$ on the optimal reproductive strategy and its interaction with the helper's fertilization capacity, $f$. Note that since the helper has the option to decide about parasitism only at time $t = 0$, $\lambda_P(t) = \lambda_{\bar{P}}(t)$ for $t > 0$. Lines represent thresholds where the helper should switch from one behaviour to the other. In the area to the left of a threshold reproductive parasitism is optimal. To the right parasitism should not be performed. Calculations are based on the basic assumptions (see Table 1). (a) $R = 0.75$; (b) $R = 0.25$.

The influence of changes in $R$ on the optimal reproductive strategy is minor compared to relative expulsion risk and relatedness (Fig. 5b). When $R$ is high, helpers should postpone reproductive parasitism. When it is low, parasitism becomes more profitable, but for small helpers only if the parasitism capacity, $f$, is high.

Our model predicts a similar pattern of low profitability of reproductive parasitism when the average reward per cycle after the helper's expulsion or death, $F$, is low. For example according to the baseline in Eq. (28) and with average relatedness, $F = 0.0396$. We present

the results of the sensitivity analysis in terms of a variation factor measuring the increase of $F$ relative to this baseline (where $\eta = 1.0$). When the future fitness $F$ is increased, e.g. to $\eta = 1.5$ ($F = 0.0594$) a recently matured helper with parasitism capacity $f > 0.25$ should



(a)



(b)



(c)

reproduce (see Fig. 5c). Thus increasing the production of breeders without the focal helper by about 50% is sufficient for the helper to risk expulsion as a consequence of parasitism. The sensitivity of the optimal strategy to this parameter is relatively low compared to the effect of $f$ (comparison not shown).

Growth costs of parasitism influence the optimal reproductive strategy of helpers strongly when $\lambda_P(0)/\lambda_{\bar{P}}(0)$ is close to 1.0 ($\lambda_P(0) \approx 0.161$), i.e. when there is no risk of being punished for reproductive parasitism. In this case, helpers should postpone parasitism until body size is large when the costs of reduced growth are high for parasitism. With moderately reduced growth, $g_P(x)/g_{\bar{P}}(x) > 0.60$, helpers should parasitize from maturity onwards. The general pattern that the model predicts is that the reproductive strategy is more sensitive to changes in parameter values of small compared to large helpers, which can expect to receive a territory of their own in the near future.
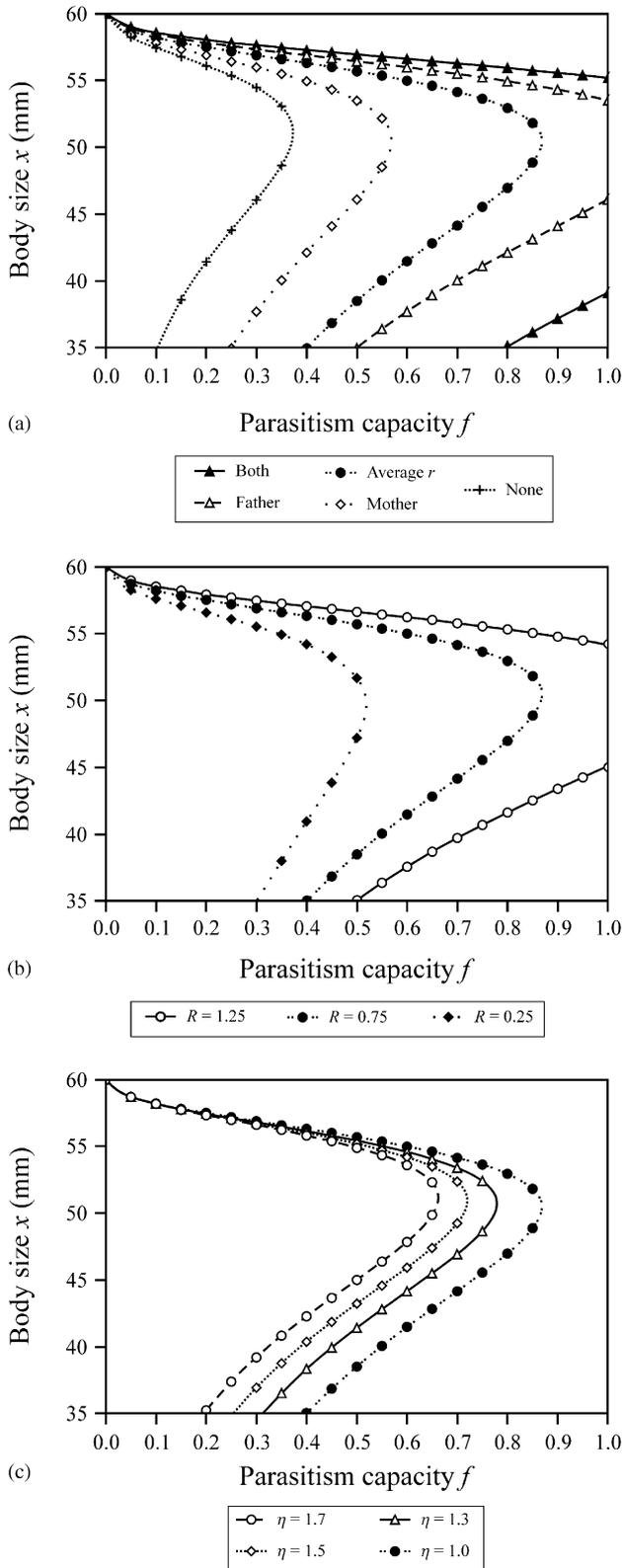
## 5. Discussion

Our model predicts that the increased probability of expulsion from the family after reproductive parasitism (punishment) and parasitism capacity are both key variables for the decision of helpers to parasitize the breeders' reproduction. The results show that if the expulsion probability of a parasitizing helper is only slightly greater than that of a non-parasitizing helper then parasitism is optimal at all sizes. As the difference between expulsion probabilities increases there are initially two thresholds, with parasitism optimal for small fish and large fish, but not optimal at intermediate size. As the difference increases further the lower threshold disappears and it is only optimal to parasitize when size is large. If the parasitism capacity is increased for given expulsion probabilities there is a transition from parasitism when large, to parasitism when large or small, to parasitism at all sizes. The two critical thresholds can be understood as follows. Mortality is greater in the aggregation than on the territory, so being

Fig. 5. The optimal reproductive strategy as a function of the helper's parasitism capacity $f$. In the area to the right of a threshold reproductive parasitism is optimal. To the left parasitism should not be performed. Calculations are based on the basic assumptions (Table 1). (a) Effect of average intra-group relatedness and relatedness in four different cases (see Table 2); both: both breeders are the helper's parents; father: only the father is present; mother: only the mother is present; none: the helper is not related to the breeders (e.g. because of replacement of breeders or because of SPS performed by the helper's father); Average $r$: male helpers' average degree of relatedness as found in the field. (b) Effect of future expected reproductive success of the helper in a territory of its own, $R$. (c) Effect of the average reward per brood cycle when the helper has ceased to care. When $\eta = 1.0$ and based on average relatedness $F = 0.0396$.

expelled imposes a cost in terms of reduced probability of surviving to the critical size. Since small helpers are unlikely to survive anyway, the cost of expulsion is less than for medium sized helpers who have a reasonable chance of survival. Large helpers are likely to be expelled even if they do not parasitize. They also have a good chance of survival in the aggregation. As a result it is worth parasitizing when large.

We conclude from our model that even helpers with a low parasitism capacity (e.g. 20% of the current clutch) should start to reproduce if their expected future fitness and the punishment risk are low (Fig. 4b). However, when the expected reproductive success in a territory of their own is high, helpers would have to fertilize at least 30 to 40% of the offspring (parasitism capacity; Fig. 4a) of a given clutch compared to the helper effect $(N_H - N_0)$ of about 47%, for parasitism to be the preferable option. These results are robust to changes in relatedness, growth costs and future reproduction by breeders without the helper.

DNA-fingerprinting data from an experimental study by Dierkes et al. (1999) revealed that the average size of parasitizing male helpers was 48.8 mm SL. On average, they sired 20.3% of the clutch and the two smaller of three parasitizing helpers were expelled from the territory. From our model we would predict an average switch size to reproductive parasitism of 57.15 mm SL, given that the helpers reacted according to average relatedness in the field, the expulsion probability observed in the lab, and basic assumptions for the other parameters. The observed size of parasitism is within the model's predicted size range of optimal reproductive parasitism if breeders without the helper would produce 1.7 times more offspring compared to solitary breeding ($F$: $\eta = 1.7$) and the future fitness of a helper in a territory of its own is low ($R = 0.25$). To test the model in detail we would need more genetic data on reproductive parasitism from the wild as well as estimates on the future expected fitness benefits $F$ and $R$.

It is interesting to consider the possibility that species with helpers might differ in parameters such as parasitism capacity and expulsion probability. It is possible that in species where the optimal strategy is to parasitize when both small and large, all individuals will be expelled while small because of their behaviour. Thus parasitism by large individuals will not be seen. In contrast, in those species where it is only optimal to parasitize when large, this behaviour will be observed. Thus we might see some species in which small male helpers start to reproduce shortly after maturity as found in many fish species (Taborsky, 1994; Taborsky, 2001) and other species in which helpers invest in cooperative brood care, long-term survival and future reproduction in a territory of their own and therefore parasitize only at a large body size. It is only in this latter group that we might expect a social queuing strategy (Kokko and Johnstone, 1999) to evolve.

Reproductive skew is a term used to indicate whether or not reproduction is shared equally amongst members of a group (for reviews see Johnstone, 2000; Reeve and Keller, 2001). Skew is said to be high if most of the breeding is monopolized by one or a few animals. Transaction models of optimal reproductive skew assume that dominants control group membership. There are two classes of transaction models: (i) Concession models assume that dominants also control reproduction and that they make reproductive concessions to increase the subordinate's incentive to stay and help (Vehrencamp, 1979; Emlen, 1982; Reeve and Ratnieks, 1993). (ii) Restraint models assume that the subordinate controls reproduction and that it is evicted by the dominant if the amount of reproduction it claims exceeds that acceptable to the dominant (Johnstone and Cant, 1999). Transactional models are game-theoretical, in that both the dominant and the subordinate maximize their inclusive fitness given the behaviour of the other. In contrast, in our model the behavioural strategy of the dominant is assumed and the subordinate maximizes its inclusive fitness given the behaviour of the dominant. Most skew models consider a single decision by the dominant and a single decision by the subordinate, whereas in our model the subordinate makes a sequence of decisions as it grows. Although our model does not correspond to any class of skew model, it does have some resemblance to restraint models in that the probability that the subordinate is evicted depends on its reproductive behaviour. Skew models envisage a single reproductive bout in which the subordinate can choose the proportion of reproduction that it attempts to obtain. In our model on any given reproductive bout the subordinate can choose either to have a proportion 0 or a proportion $f$ of the reproduction, but can make repeated choices between these options as it grows.

The restraint model of Johnstone and Cant (1999) predicts that the subordinate's share in reproduction increases when relatedness, ecological constraints that limit dispersal, or the productivity of the group increase. Our model predicts that the subordinate's share in reproduction decreases when relatedness increases. A possible reason for this difference is that in analysing our model we have changed relatedness without changing expulsion probability, whereas game theoretic models allow this probability to depend on relatedness. A reduction of the expected reproductive success at independence (equivalent to high ecological constraints) leads to an increased investment in reproductive parasitism in our model. If growth costs are reduced, which in turn increases the helper size-dependent offspring survival (and thus group productivity), then parasitism by helpers is favoured in our model. These two predictions are comparable to those of the restraint

model. In addition, our approach predicts that a high future indirect inclusive fitness benefit and a high parasitism capacity may advance reproduction by subordinates.

Our model predicts that male helpers should base their decision to parasitize primarily on the presence of their father, while the presence of their mother should have a lower influence on this decision. When the father is still present, helpers should invest more in cooperative alloparental care and postpone reproduction. In the southern *N. pulcher* population, it is possible that the female breeder is the mother, sister or half-sister of large helpers while the degree of relatedness between subordinates and male breeders is apparently very low (DNA-microsatellite analysis by Dierkes, et al., unpubl. data) and negative inbreeding effects on fitness are not known in this species. Stiver et al. (unpubl. data) showed that the helpers invest more in direct brood care when they are only related to the dominant male but that they invest more in defence when they are unrelated to it. The results of our model in conjunction with these empirical findings suggest that male helpers might invest in direct brood care of kin of their father but increase defence for being allowed to breed and stay when unrelated to the dominant male. For high parasitism capacities, parasitizing should be the best strategy from maturity onwards when only the mother or none of the genetic parents are present. This suggests that if helpers can choose the parasitism capacity, $f$, they should choose a high value of this variable if the father has disappeared from the territory, possibly reversing the reproductive skew, without necessarily reversing the dominance hierarchy. A pattern of reversed reproductive skew has been found in male spotted hyenas (Engh et al., 2002), where immigrant males that are subordinate to the alpha male sire 97% of the offspring.

We have assumed that $f$ is independent of size once a male is sexually mature. This may not be the case. The reproductive success of externally fertilizing male fish depends on (i) the number of sperm released, (ii) the distance to eggs at spawning and (iii) the timing of sperm release relative to competitors (Taborsky, 1998). In *N. pulcher* there is a negative correlation between gonadosomatic index and the condition factor of mature helpers (Neat et al., unpubl. data), which suggests that an increased investment in gonads will reduce growth and body condition. Thus, small helpers might have a low parasitism capacity because of limitations imposed by gonad size and significant long-term fitness costs.

Another limit of our model is that the expulsion probability is an input rather than something that the dominant individuals can decide about. In reality, helper behaviour and expulsion probability are likely to co-evolve. Dominant breeders may control the reproductive distribution within the family by varying the expulsion probability of helpers, which in effect decides about family membership of subdominant individuals (Taborsky, 1985) and therefore about group composition. Submissive and helping behaviours are costly in *N. pulcher* in terms of time and energy, (Taborsky and Grantner, 1998) and may reduce growth (Taborsky, 1984). This means that if breeders are selected to prevent helpers from simultaneous parasitic spawning, they should either punish them for parasitism (i.e. expel them), or impose high growth costs on them, for example by demanding high levels of submissive behaviour. A further limitation of our model is that relatedness is held constant during growth. In reality it tends to decrease over time as one or more parents die and are replaced.

Nonacs (2000) pointed out that social behaviour is multidimensional and should be quantified by a measure of reproductive benefit relative to both total group output and the proportion of time spent in the social group. Our model predicts that the participation in reproduction of a subordinate in the group depends on its size and hence its share in reproduction will change from one reproductive cycle to another. This has been confirmed by Dierkes et al. (1999). Empirical measures of total group output might not be easy to obtain from all systems. Thus, it may depend on the studied species whether a measure of reproductive skew relates to a certain life history phase or to lifetime reproduction of an individual. The model presented here suggests that the distribution of reproduction for a given clutch may vary with the parasitism capacity and that overall reproductive skew, which is the result of optimal reproductive parasitism, may depend on the body size of a helper.

From our sensitivity analysis we conclude that in descending order of importance, punishment by dominants, relatedness, parasitism capacity, future expected own reproduction, future reproduction by breeders and growth costs, should determine whether reproductive parasitism is a beneficial alternative to delayed reproduction. When relatedness is very high, the future reproduction by breeders after the helper has left the group is predicted to have a higher influence on the optimal strategy than the expected future reproduction of the helper on a territory of its own. From the predictions of our model, we would expect a high reproductive participation of subordinates in groups with low breeder-helper relatedness, low dispersal of reproducing subordinates as a result of expulsion by breeders from the group, and high capacities of subordinates to reproduce. The predictions of our model may be tested in the field by estimating how parasitic spawning depends on size under various conditions. The proportion of offspring sired by helpers and data on gonad size together with breeder-helper size differences and distances to the breeding place in space or time may serve as a measure of the parasitism capacity.

It would be interesting to extend our modelling approach to a full dynamic game between dominants and subordinates, and to use this approach to study reproductive strategies of subordinates in cooperatively breeding birds and mammals. Mortality and also the helper effect might be size-dependent whereas growth declines to zero at some time after sexual maturity in most of these vertebrates (Stearns, 1992; Cichoń and Kozłowski, 2000). Other measures representing competitive ability, such as age, weight or condition may serve as relevant state variables instead of length, and may easily be incorporated in the model. We encourage future studies to focus on expulsion risk and variation in the state of subordinates. Analysing questions of reproductive share in a dynamic framework may help us to understand the high variation in reproductive success and cooperative behaviour that has been found between and within species. The social relationships in cooperative breeders are probably more complex than assumed in traditional models of reproductive skew, because costs and benefits to dominants and subordinates vary during their life histories and are subject to interactions at different levels.

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## Appendix

We assumed that a helper is certainly expelled for $x \geqslant x_c$ and $0 \leqslant t \leqslant T - 1$, which led to Eqs. (15), (16), (24) and (25). In doing so, we implicitly assumed that the expulsion probability is discontinuous at size $x_c$, i.e. it jumps to 1. This discontinuity produces modelling artifacts close to size $x_c$. To remove these we introduce a weight function

$$\omega(x) = \frac{1}{1 + c(x - x_c)^2}. \tag{A.1}$$

The state- and time-dependent expulsion probabilities for non-parasitizing and parasitizing helpers are then calculated as

$$\lambda'_.(x, t) = [1 - \omega(x)]\lambda_.(t) + \omega(x). \tag{A.2}$$

This function does not alter the main characteristics of our model away from size $x_c$.

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