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Evolution of Alternative Reproductive Strategies: Frequency-Dependent Sexual Selection in Male Bluegill Sunfish

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Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish

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SUMMARY

This study provides empirical evidence in a wild population for frequency-dependent sexual selection between alternative male reproductive strategies. The bluegill sunfish (*Lepomis macrochirus*) has two male reproductive strategies, cuckolder or parental, used by different males to compete in fertilizing the same eggs. As the density of cuckolders in colonies of parental males increases, the average mating success of cuckolders initially peaks but then declines. The cuckolder density at which their success peaks is determined by ecological characteristics of each colony. A theoretical analysis assuming random and omniscient cuckolder distributions among ecologically different colonies shows that cuckolders will fertilize decreasing proportions of eggs, relative to parental males, as cuckolders increase in frequency in the population. This supports evolutionary models that assume negative frequency-dependent selection between the competing strategies. Cuckolder and parental strategies may therefore have evolved as an Evolutionarily Stable State (ESST).

1. INTRODUCTION

Polymorphisms in male behaviour and life history are found in many species where males compete for access to mates. Examples include antlered and antlerless red deer (Darling 1937), lekking and satellite ruff (van Rhijn 1983; Lank & Smith 1987), territorial and streaker wrasse (Warner 1984), parental and cuckolder sunfish (Gross 1982), and adult and precocious salmon (Jones 1959; Gross 1985; Maekawa & Onozato 1986). In many of these polymorphisms, one phenotype is specialized in fighting for mates while the alternative phenotype, evolved secondarily, is specialized in sneaking. This paper addresses the evolutionary stability of such reproductive polymorphisms.

For a reproductive polymorphism to be evolutionarily stable, a mechanism must exist for the alternatives to have equal fitnesses. Theoretical research suggests that alternative reproductive strategies may evolve through negative frequency-dependent sexual selection (Gadgil 1972; Gross & Charnov 1980; Charnov 1982; Maynard Smith 1982; Gross 1984, 1991; Parker 1984). Imagine that a strategy's mating success depends on its frequency in the population. When rare, the alternative strategy has greater success than the primary strategy, and therefore invades. However, if the alternative strategy's mating success is negatively frequency-dependent (Partridge & Hill 1984; Knoppien 1985), such that with increasing frequency its fitness declines *relative* to that of the primary strategy, an evolutionarily stable frequency may exist where both strategies have equal fitnesses.

At present there is no empirical demonstration of frequency-dependent sexual selection for a wild population (see Partridge 1988). Instead, research has focused on documenting density-dependent selection, usually in an artificial environment. For example, many salmonid species have males that mature at different ages, with older males fighting for mates while younger males sneak matings (Gross 1984). Using electrophoresis, Maekawa & Onozato (1986) and Hutchings & Myers (1988) provide empirical evidence that the success of sneaking males decreases with their density at the oviposition site. Thus with increasing numbers of sneakers, the absolute success per sneaker decreases. Such negative density dependence is not equivalent, however, to negative frequency-dependent selection. The latter requires a decline in the average success per sneaker phenotype *relative* to the average success per fighter phenotype. For example, if a sneaker fertilizes 10% of the eggs when alone with a fighter male at the oviposition site, but only 6% when in a group of ten sneakers, success is negatively density dependent. The fighter male in this example will fertilize 90% and 40% (100% − (10 × 6%)) of the eggs respectively. Therefore the average success per sneaker phenotype relative to that per fighter phenotype has actually increased from 11% (10%/90%) to 15% (6%/40%). This example illustrates that the evolutionary fitness of sneakers may increase with their frequency even though their absolute success declines with their density.

It is important to consider mating sites as subunits from which the cumulative success of strategies is determined at the population level. Subunits will often differ from each other ecologically, and thus the relation between mating success and density may not be constant. Subunits have not been considered in previous studies because manipulations were carried out in artificial environments. The purpose of this paper, therefore, is to outline a test for negative frequency-dependent sexual selection in a wild population. It also presents evidence for both density-dependent and frequency-dependent mating success while incorporating ecological variation in breeding sites. The alternative reproductive strategies studied here are those of the cuckolder and parental males in bluegill sunfish, *Lepomis macrochirus*.

Alternative strategies in male bluegill sunfish

The reproduction of bluegill, an endemic freshwater species of North America, has been studied for 17 consecutive years in Lake Opinicon, near Kingston, Ontario, Canada (see Gross 1979, 1980, 1982, 1984, 1991; Gross & Charnov 1980; Kindler *et al.* 1989). These studies provide ample data for outlining the breeding dynamics of a male polymorphism involving 'parentals' and 'cuckolders.'

Parental male bluegill delay maturity until age seven or eight years. During the summer breeding season, parental males fight among themselves for space to construct a nest within a developing colony. These nests are shallow depressions in the lake bottom made by sweeping motions of the caudal fin. The resulting colonies vary in water depth and cover provided by vegetation and debris. Females arrive at the colony in a school, and the parental males court and subsequently spawn with them. Spawning involves a female entering a nest and repeatedly releasing a small batch of eggs (about 12) using a characteristic dipping motion. The male paired with her fertilizes the eggs during each dip. A male may receive eggs from many different females, accumulating some 30000 eggs in his nest. A female may also spawn in many nests. Spawning within the colony occurs quickly, usually finished within a day. Females then leave the colony while the parental males remain at their nests to provide the care necessary for brood survival. Owing to the dynamics of female arrival, males within a colony and colonies within the lake are highly synchronized in spawning behaviour.

Cuckolder males have a different life history. They mature precociously, usually at age two. Rather than build nests, they distribute themselves among colonies during parental nest-building. When the females arrive, the cuckolders move among the nests within a colony tracking spawning opportunities. The smallest cuckolders behave as sneakers, penetrating the parental male's defence of his nest boundary, and spawning directly over the eggs during the female's dip. Larger cuckolders, four or five years old and about the size of females, act as satellites. These satellites hover in the colony, and follow true females into the nest by mimicking female behaviour. Success depends on deceiving the parental male, and pairing with the female during her dips. Both sneaking and mimicry are ontogenetic tactics within a distinct cuckolder strategy; these males do not live beyond age six. Although only 11–31% of bluegill males in the population mature as cuckolders, the earlier maturity and therefore higher probability of surviving to breed results in mature cuckolders outnumbering mature parental males by a ratio of approximately six to one.

Unlike salmon where several males simultaneously release large clouds of sperm over a single batch of eggs (Jones 1959), sperm competition is probably not a major factor in determining mating success between the parental and cuckolder strategies. Instead, mating success is determined by the behavioural ability to pair with the female during her dip – called 'pairing success'. For parental males, pairing success is determined by their ability to attract females to their nest and then control access to the dips. This control is achieved through guarding against cuckolders by patrolling the nest boundary to detect and chase sneakers and by screening female-sized individuals to detect and rout satellites. Parental males can also control the female dipping behaviour by biting the female. In so doing, the parental risks the female leaving the nest to spawn elsewhere. For cuckolders, pairing success depends upon circumventing the parental male's defence and pairing with the female, quickly placing sperm over the eggs. Both sneakers and satellites use surrounding vegetation and debris as cover from detection and chases by parental males. Cover is also used to avoid piscivorous predators that enter the colonies to feed on the smaller-bodied cuckolders.

In a study of pairing success at seven colonies (Gross 1982), cuckolders attempted to intrude into the nests during nearly 60% of the female dips. Most of these attempts were blocked by parental males, and only 14% of all female dips were successfully paired by cuckolder males. Females did not avoid cuckolder males, but rather spawned readily with them even while the parental male was chasing egg predators or other cuckolders. Thus the primary determinant of cuckolder pairing success was avoiding the parental male. This ability varied among colonies, and was affected by ecological factors as well as interactions among cuckolders themselves. As a consequence, the pairing success at the seven colonies ranged from about 3% to 34% of female dips.

Gross & Charnov (1980) and Gross (1982) proposed that the cuckolder and parental strategies in bluegill may coexist as an Evolutionarily Stable State (ESST), where both strategies have equal lifetime fitnesses at the balance point. An important assumption in their ESST models is that strategy fitnesses are regulated by negatively frequency-dependent sexual selection. This would occur if: (i) the pairing success of cuckolders decreases with their density within colonies; and (ii) the distribution of cuckolders among colonies, combined with the density dependence within colonies, results in the relative pairing success of cuckolders to parentals decreasing with increasing cuckolder frequency in the population.

In this paper, cuckolder density is experimentally manipulated at nests within four natural colonies and

Table 1. *The four colonies in Pen Bay*

(Data are mean ± s.e. unless otherwise indicated. The percent distribution of parental males among the four colonies is given.)

variable	colony A	 B	 C	 D
water depth cm	51.2 ± 2.6	27.8 ± 2.6	60.0 ± 5.9	97.2 ± 4.0
cover %	87.9 ± 2.6	55.0 ± 5.0	18.7 ± 4.3	25.8 ± 2.9
parental males n (%)	12 (19.4)	14 (22.6)	12 (19.4)	24 (38.7)
experimental range in cuckolder density per nest	1–11	1–10	1–9	1–12
dips observed:				
total	408	304	243	723
per cuckolder density	40.8 ± 6.9	33.8 ± 9.1	30.4 ± 6.7	60.3 ± 6.8

their pairing success is quantified to examine negative density dependence within the colonies. Since cuckolder distribution among colonies is unknown, two theoretical distributions – random and omniscient – are used to test the density dependence results for negative frequency-dependent mating success at the population level. The random distribution is a conservative assumption that cuckolders do not adjust their numbers among colonies to maximize mating success. The omniscient distribution is a liberal assumption that cuckolders can adjust their distribution among colonies to perfectly maximize their possible mating opportunities.

2. STUDY SITE AND METHODS

The study included all four bluegill colonies, A to D, formed within Pen Bay of Lake Opinicon during July 1981. Our studies both before and after this date suggest that the breeding success observed within these colonies is representative of the population at large. The Pen Bay colonies were therefore studied as ecological subunits within the population.

Each colony was ecologically characterized by the amount of cover afforded cuckolders and by water depth. To quantify cover, a 630 cm^2 plexiglass sheet ruled with a black-and-white checkerboard pattern of 1 cm squares was held 15 cm from a nest's edge. A SCUBA diver, looking out from the centre of the nest, counted the number of white squares not blocked by cover, and repeated this count in three other directions from the same nest centre. The proportion of squares obscured by vegetation or debris was converted to percent cover. Six nests chosen randomly within each colony were sampled and their results pooled to estimate the average cover in the colony. Water depth was measured from the surface to each nest edge.

Skin divers at each colony observed the spawning of cuckolders and parentals to quantify pairing success. As in Gross (1982), success was credited to the phenotype, either cuckolder or parental, paired with the female when she dipped. In only 18% of dips were both male types equally paired to the female; success was then randomly assigned.

To test for density-dependent success within each colony, cuckolder densities were experimentally manipulated by selectively removing individuals from nest sites with a dipnet. This resulted in a broad range of cuckolders per nest site within each colony. The number of cuckolders per nest site ranged from 1 to 12, depending on the colony (table 1; no observations were obtained in colonies A, B and C for 4, 7 and 2 cuckolders per nest, respectively). Neither observation nor removal caused any apparent disturbance to spawning activity.

To test for frequency-dependent success in the overall population, the following mathematical treatment was applied to the data on density-dependent pairing success from the four colonies. The average success of the cuckolder strategy within Pen Bay is a function of the sum of cuckolder successes within each colony. The success within each colony depends on cuckolder density and is therefore a function of the total number of cuckolders in the population and their distribution among the colonies. Thus, the average success of the cuckolder strategy is calculated from

$$\bar{S}\mathrm{c} = \sum_{i=\mathrm{A}}^{\mathrm{D}} (P\mathrm{c}_i)\,(\bar{S}\mathrm{c}_i), \tag{1}$$

were $P\mathrm{c}_i$ is the proportion of cuckolders in the population that go to the ith colony, and $\bar{S}\mathrm{c}_i$ is the average success per cuckolder in the colony. Similarly, the average success of the parental strategy is

$$\bar{S}\mathrm{p} = \sum_{i=\mathrm{A}}^{\mathrm{D}} (P\mathrm{p}_i)\,(100\,\% - \bar{S}\mathrm{c}_i), \tag{2}$$

where $P\mathrm{p}_i$ is the proportion of parentals in the population that go to the ith colony. Therefore, the average pairing success of the cuckolder strategy ($\bar{W}\mathrm{c}$) *relative* to the average pairing success of the parental strategy ($\bar{W}\mathrm{p}$) for different frequencies of cuckolder and parental males in the population is

$$\bar{W}\mathrm{c}/\bar{W}\mathrm{p} = (N\mathrm{c}/N\mathrm{p})\,(\bar{S}\mathrm{c}/\bar{S}\mathrm{p}), \tag{3}$$

where N is the number of each kind of male in the population.

Unlike the stationary parental males, whose proportional distribution among colonies is easily quantified ($P\mathrm{p}_i$), the mobile cuckolders are difficult to follow and only their density at specific nest sites, not their proportional distribution among colonies ($P\mathrm{c}_i$), can be directly quantified. Therefore, to calculate how cuckolder and parental male success ($\bar{W}\mathrm{c}/\bar{W}\mathrm{p}$) changes

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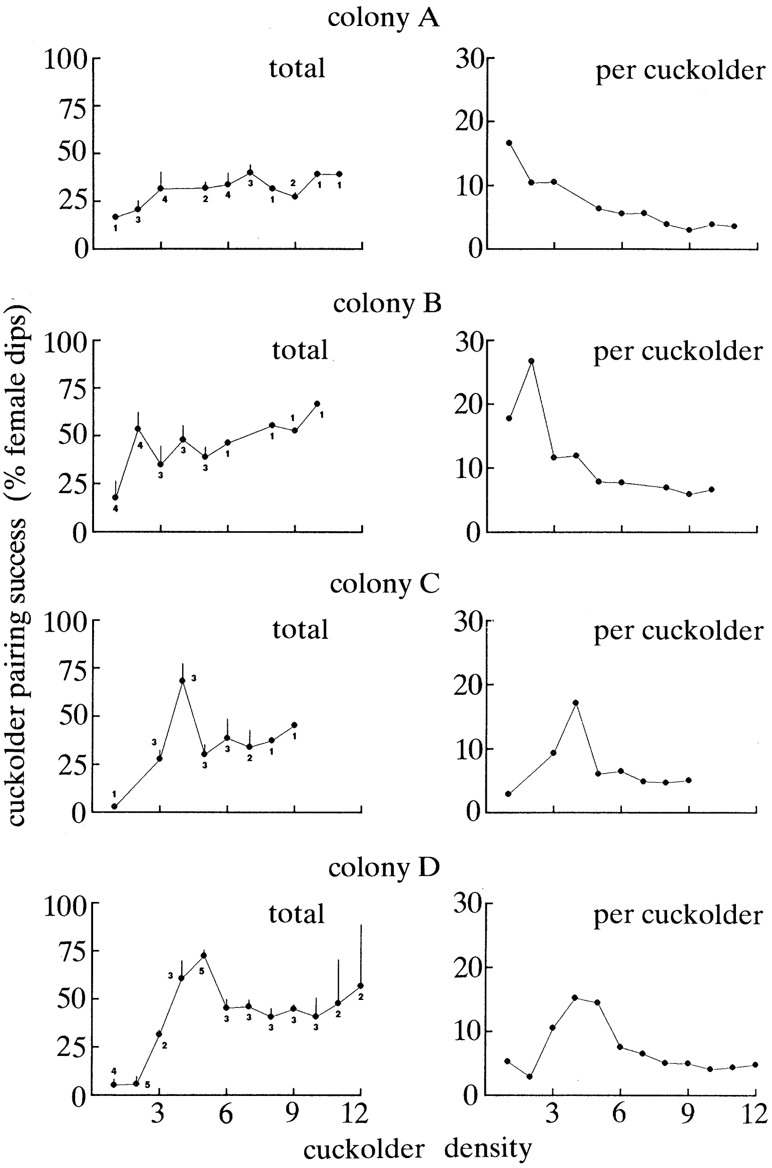

Figure 1. The relation between cuckolder pairing success and cuckolder density (number of cuckolders) at nests in four bluegill colonies, A–D. Both the total success of cuckolders at each density and the average success per cuckolder (total success/number of cuckolders) are plotted. Number of nests sampled at each cuckolder density, and one-half s.e., are shown with the data; individual nests were used more than once when spawning occurred under different cuckolder densities. Percent cover at the colonies is: A = 88 %, B = 55 %, C = 19 %, D = 26 %.

with their relative frequency (Nc/Np), two theoretical distributions – random and omniscient – were used. These theoretical distributions should bracket the true distribution of cuckolders (see, for example, Gross 1984).

In the random distribution, cuckolders disperse among colonies in direct proportion to parental males. Thus, Pc_i is always equal to Pp_i. This assumes that cuckolders do not adjust their distribution among colonies to reflect differences in success with cuckolder density, a conservative assumption that should give a minimum estimate of $\bar{W}c/\bar{W}p$.

In the omniscient distribution, cuckolders possess complete knowledge of how their pairing success varies with density in colonies. They distribute themselves among the colonies such that $\bar{W}c/\bar{W}p$ is always maximized. This assumes that cuckolders approximate an ideal-free mating distribution (Fretwell & Lucas 1970), a liberal assumption as there is both despotic aggression among cuckolders and varying predator pressure among colonies (Gross 1982). The test for negative frequency-dependent selection therefore includes both a minimum (random distribution) and a maximum (omniscient distribution) estimate of relative success ($\bar{W}c/\bar{W}p$) as cuckolder and parental frequency (Nc/Np) change in the population.

3. RESULTS

(*a*) *Colonies*

The four colonies, located in different areas of Pen Bay, differed ecologically in average water depth and cover afforded to cuckolders (table 1; ANOVA depth, d.f. = 3,20; $F = 155$; $p < 0.001$. ANOVA cover, (% data arcsine square-root transformed) d.f. = 3,20; $F = 68$; $p < 0.001$). However, these variables were not related to the highest natural density of cuckolders observed at a nest in each colony (Spearman rank correlations: depth $r = 0.5$, $p > 0.5$; cover $r = 0.5$, $p > 0.5$). The number of parental males nesting in the colonies was also unrelated to these variables (depth $r = 0.80$, $p > 0.2$; cover $r = 0.4$, $p > 0.5$). Finally, water depth and cover were not significantly correlated ($r = 0.5$, $p > 0.5$).

(*b*) *Density-dependent pairing success*

Cuckolder pairing success was density dependent within each colony (figure 1). However, the density providing peak average success per cuckolder was negatively correlated with the amount of cover at the colony (Spearman rank correlation, $r = -0.99$, $p < 0.02$). Thus in colony A, with a high of 88% cover, average pairing success per cuckolder peaked at 17% of female dips when only a single cuckolder was present at the nest site and declined to 4% of dips with 11 cuckolders present. By contrast in colony B, with 57% cover, there was an initial increase in average pairing success with density. Here, a single cuckolder achieved 18% of the female's dips, but two cuckolders at the nest each achieved 27%. Success then declined to near 7% with 10 cuckolders present. A similar pattern of initial increase in average pairing success followed by negative density dependence occurred in colonies C and D. However, in these colonies the sparser cover moved the peak yet further to the right.

The decline in average cuckolder success at densities above the peak was related to an increase in the occurrence of simultaneous intrusions, and thus competition among the cuckolder males (cuckolder density versus percent simultaneous intrusions; $n = 9$, $r = 0.894$, $p < 0.01$). For example, at the density of peak success in each of the four colonies, cuckolders competed among themselves for the same dip in only 7% of pairings on average. Beyond this peak, simultaneous intrusions in the four colonies increased to 28% of pairings. At the highest cuckolder densities seen in the colonies, as many as eight individuals were observed entering the nest to fertilize the same dip. Thus the cuckolder males at high densities experienced stronger competition among themselves, than with the parental male. Aggression also increased significantly among cuckolders when their density exceeded peak success within the colonies (chases per cuckolder per minute relative to number of cuckolders present; before peak = 0.3 ± 0.3 s.e., after peak = 1.2 ± 0.2, $t = 4.8$, $p < 0.01$; data pooled over colonies B, C and D, $n = 97$).

Parental males directed aggression not only towards cuckolders, chasing them from the nest area, but also towards the spawning female. Bites to the female slowed her dipping rate (female dips per minute without male aggression = 5.8 ± 0.6 s.e., $n = 51$; with aggression = 4.8 ± 0.4, $n = 28$; $t = 4.9$, $p < 0.05$), and the relative pairing success of parental males increased (pairing success at 5.8 dips per minute = 45%; at 4.8 dips = 82%; $n = 79$, $\chi^2 = 10.26$, $p < 0.01$). However, aggression also increased the probability of females abandoning the nest (bites to female per minute versus total minutes female spawned; $n = 23$, $r = -0.728$, $p < 0.001$). At the highest cuckolder densities, parental males were observed to escalate their aggression to a level where the female was driven from the nest. Cuckolders at such a nest then dispersed to nests with fewer cuckolders.

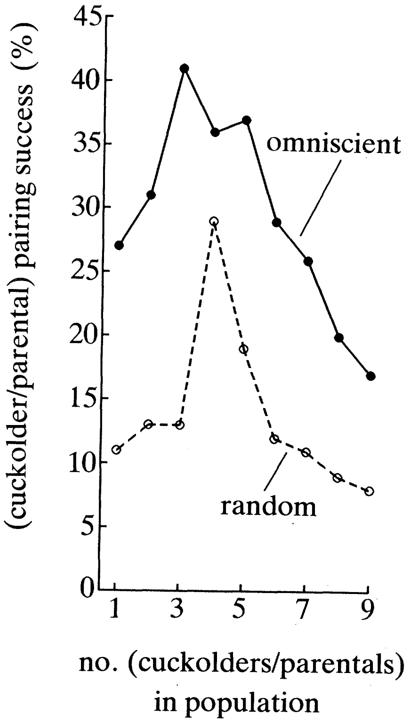

Figure 2. The relative pairing success of cuckolder and parental males ($\bar{W}c/\bar{W}p$) across a range of frequencies (Nc/Np) in the population. Two curves have been calculated based on assumed cuckolder distributions among the bluegill colonies in figure 1: omniscient and random (see text for details).

(*c*) *Frequency-dependent pairing success*

The theoretical calculations of the random and omniscient cuckolder distributions among the four colonies show that the relative average pairing success of cuckolder and parental males depends upon their relative frequencies in the population (figure 2, example calculations in Appendix 1). With an omniscient distribution, and an equal frequency of cuckolder and parental males in the population ($N\text{c}/N\text{p} = 1$), cuckolders will obtain about 27% as many pairings as parental males. This increases to 41% when cuckolders outnumber parentals 3:1 ($N\text{c}/N\text{p} = 3$), but declines to 17% at 9:1 ($N\text{c}/N\text{p} = 9$).

As expected, cuckolders are less successful with a random distribution among colonies. With an equal frequency of cuckolder and parental males in the population ($N\text{c}/N\text{p} = 1$), cuckolders obtain only 11% of the success of parentals. This increases to 29% the success when cuckolders outnumber parentals 4:1 ($N\text{c}/N\text{p} = 4$), but declines to 8% at 9:1 ($N\text{c}/N\text{p} = 9$). Therefore both distributions result in negative frequency-dependent success once cuckolder frequency becomes high in the population.

4. DISCUSSION

The experimental manipulations of cuckolder density within bluegill colonies of Lake Opinicon have shown that cuckolder pairing success is density dependent, but that there is a unique density at each colony which maximizes individual success. The population is therefore heterogeneous in the relation between cuckolder density and success. Consequently, no single colony can provide an adequate test of frequency-dependent selection between the cuckolder and parental strategies within the population.

The occurrence of unique densities where cuckolder success peaks is largely due to ecological differences in cover among colonies. Cover is important because it determines how closely cuckolders can approach a nest. Close proximity improves a cuckolder's ability to monitor spawning activity, and also aids his ability to pair with the female by reducing the length of his exposure to the parental male's aggressive defence. In colonies with abundant cover, additional cuckolders at the nest site increase competition, and therefore average cuckolder success is negatively density dependent immediately. But when cover is sparse, cuckolders are unable to stay close to the nest. Additional cuckolders then make a positive contribution to individual mating success by indirectly creating opportunities for each other to intrude through distraction of the parental male. Thus individual cuckolder success in colonies with sparse cover is positively density dependent at first. Because increasing cuckolder density eventually creates more competition than distraction, individual success then becomes negatively density dependent. Each colony thus has an optimum cuckolder density, dependent on cover, at which cuckolder pairing success is maximized.

The colony-specific optimums in cuckolder density will be a key factor in how natural selection favours cuckolders to distribute themselves among colonies. However, there are several constraints that may also influence cuckolder distribution, preventing the fitness of the cuckolder strategy from being maximal. For example, predators hunting in deeper colonies (Gross 1982) may favour the crowding of cuckolders into shallower colonies with more cover. A trade-off between survival and reproductive success will result in lower individual pairing success owing to increased competition (for example, see Lima & Dill 1990). Another constraint on distribution is the information available to cuckolders about the relative advantage of different colonies. Since parental males use traditional nesting sites, cuckolders could be aware of these locations and the ecological situations there. Cuckolders could also know their own abundance and density as cuckolders often travel in schools. A third factor that may influence distribution is despotic behaviour by fellow cuckolders. Once the optimum density was reached, cuckolders were observed to become increasingly aggressive towards each other; larger individuals sometimes drove smaller individuals from nest sites. This behaviour may displace some cuckolders to alternative colonies where individual success is lower. Such a despotic distribution (Fretwell & Lucas 1970) would not only increase the variance among individuals, but it could also decrease the mean fitness of the strategy.

Cuckolders will therefore distribute themselves among colonies based on the above constraints. How well they do this to maximize their own success ultimately determines the cumulative success of the cuckolder strategy itself and thus its fitness relative to the parental strategy.

Our theoretical model of an omniscient distribution allowed cuckolders to distribute themselves according to the unique density-dependent relations within colonies, free of any constraints. In this case, the marginal value of the colonies is reduced equally and the fitness of the cuckolder strategy is as high as it can possibly be. In our random distribution, cuckolders followed the dispersion of parental males regardless of ecological differences among colonies. Thus cuckolders were not allowed to adjust their densities to maximize their mating success. Using the omniscient distribution, on average the cuckolder strategy achieved 15% more pairing success relative to the parental strategy than did the random distribution (figure 2). This shows that the distribution pattern can have a significant effect on relative fitnesses of the strategies. The analysis also showed, however, that at high cuckolder frequencies, the cuckolder's strategy's fitness declines relative to the parental strategy's fitness in *both* distributions. This shows that as their frequency increases, there is greater within-strategy competition among cuckolders than between the cuckolder and parental strategies themselves. Moreover, the within-strategy competition cannot be beaten by an omniscient distribution. Therefore, parental males are always able to maintain sufficient paternity to cause average cuckolder success to decline as cuckolder density increases.

What prevents parental males from maintaining their paternity completely? The explanation must involve the time constraint under which females operate during spawning. Female spawning behaviour has evolved under selection for synchronous spawning to minimize brood predation (Gross & MacMillan 1981). Spawning in a colony occurs in a short time span, and females do not tolerate much limitation of their dipping rate by aggression from a parental male. Parentals are thus constrained in their ability to control the female's spawning and must therefore trade off loss of fertilizations to cuckolders with fewer eggs spawned into their nest. They can forfeit fertilization of some dips to cuckolders while allowing the female to spawn rapidly, or they can slow the female's dipping rate for better control of the fertilizations but receive fewer eggs and risk female desertion. When parental males cannot maintain this compromise at extreme cuckolder densities, it becomes more favourable for the parental male to abort a spawning by driving the female from his nest rather than forfeiting all fertilizations of her dips to cuckolders.

Therefore, the time constraint on female spawning behaviour may prevent parental males from monopolizing all the spawnings, evolutionarily allowing cuckolders to exist. But as cuckolder frequency increases, the number of parental males must decrease and so too the number of alternative nests available to females. As alternative nests become less available, female choosiness must, on average, decrease. This would allow the parental male to control more of the spawning. It is this linkage among the constraints and tactics of female, parental, and cuckolder bluegill that permits existence of an alternative male reproductive strategy.

The life-history models of Gross & Charnov (1980) and Gross (1982) predict that the ESST frequency of cuckolder and parental males will exist where their lifetime fitnesses are equal. This occurs when the proportion of males in the population that are cuckolders, q, is equal to the proportion of eggs in the population that cuckolders fertilize, h (i.e. $q = h$). In Lake Opinicon, the age class at which most cuckolders first mature is age two, and q is about 11–31 % (95 % binomial confidence interval; Gross 1982). At this frequency, the earlier sexual maturity of cuckolders and decreased survivorship of males in the parental life history results in a ratio of about six mature cuckolders to one mature parental male in the breeding population. Referring to figure 2, this 6:1 ratio produces a mating success of cuckolders remarkably close to the value of h that results in equal lifetime fitness. For example, h ranges from 11 % to 23 % in the random and omniscient distributions, respectively, when cuckolders outnumber parental males six to one (to calculate h, the y-axis is converted from relative pairing success to percent of total pairings; e.g. h for the omniscient distribution is calculated by converting the 29 % on the y-axis to $29/[100+29] = 23\% = h$). Because h increases relative to q at lower cuckolder frequencies, and h decreases relative to q at higher cuckolder frequencies, the frequency-dependent sexual selection in Lake Opinicon can hold the two strategies at an ESST balance point.

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APPENDIX 1

Both the random and omniscient cuckolder distributions are calculated from $Np = 62$ (the total number of parental males in the Pen Bay population). The parental distribution, Pp_i, is the empirical distribution observed among the four colonies (table 1). The number of females spawning in colonies is assumed to follow the parental distribution. To calculate the relative success of the cuckolder and parental strategies from the random distribution, let $Pc_i = Pp_i$. For example, with equal numbers of cuckolder (62) and parental (62) males in the population, $Nc/Np = 1$; Pc_A (proportion of cuckolders at colony A) $= Pp_A = 0.194 = 12$ males; $Pc_B = Pp_B = 0.226 = 14$ males; $Pc_C = Pp_C = 0.194 = 12$ males and

$Pc_D = Pp_D = 0.387 = 24$ males. In this case there is one cuckolder at each nest of a parental male. The empirically measured pairing success per cuckolder in figure 1 shows that $\bar{S}c_A = 16.6$, $\bar{S}c_B = 17.7$, $\bar{S}c_C = 2.9$ and $\bar{S}c_D = 5.3$. Entering these values into equation (1) gives 609.0, equation (2) is 5592.4 and equation (3) is 0.109. Thus with $Nc/Np = 1$, a cuckolder male in a random distribution averages 11% the success of a parental male in the population. Similar calculations were made for all $Nc/Np \leqslant 9$, giving the data plotted in figure 2.

The relative success of the cuckolder strategy in the omniscient distribution is calculated by varying Pc_i independently of Pp_i, and maximizing equation (1) by simulation. For example, with $Nc/Np = 1$, the distribution of cuckolders among colonies that will maximize equation (1) is: $Pc_A = 0.032$ (1 cuckolder at 2 nests); $Pc_B = 0.452$ (2 cuckolders per parental); $Pc_C = 0.520$ (4 cuckolders at 8 nests) and $Pc_D = 0$ (no cuckolders go to colony D). It follows that equation (1) = 1326.8, equation (2) = 4873.2 and equation (3) = 0.272. Thus with $Nc/Np = 1$, a cuckolder male in the omniscient distribution averages 27% the success of parental males in the population (figure 2). For a second example, consider $Nc/Np = 3$ (3 cuckolders per parental male in the population). The cuckolder distribution maximizing equation (1) is now: $Pc_A = 0.065$ (1 cuckolder per parental); $Pc_B = 0.151$ (2 cuckolders per parental); $Pc_C = 0.258$ (4 cuckolders per parental) and $Pc_D = 0.527$ (4 cuckolders per parental at 22 nests and 5 cuckolders per parental at 2 nests). Equation (3) = 0.406. Therefore, with cuckolder males outnumbering parental males 3:1, a cuckolder male in an omniscient distribution averages 41% the success of a parental male in the population. Similar calculations were made for all $Nc/Np \leqslant 9$.