Cryptic female choice: frogs reduce clutch size when amplexed by undesired males

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In species with internal fertilization, females can 'cryptically' choose (e.g. through sperm selection) which individuals sire their offspring, even when their overt preferences for copulatory partners are overrun by male–male competition and sexual coercion. The experiment presented here reveals that control of paternity after copulation has begun is also possible in species with external fertilization. Females of the hybridogenetic *Rana lessonae–Rana esculenta* (*LL–LR*) waterfrog complex adjust their clutch size in response to mate type: they release fewer eggs when amplexed by hybrid *LR* males—who jeopardize successful reproduction—than when amplexed by parental *LL* males. This reduction in the number of eggs laid can increase a female's residual reproductive value through a second mating in the same breeding season or a larger clutch size in the next year. We argue that cryptic female choice through clutch size adjustment (i) may have evolved more often than previously assumed, and (ii) can arise even where females mate only once during a reproductive period.

Keywords: anurans; cryptic female choice; external fertilization; male–male competition; sexual selection; clutch size adjustment

1. INTRODUCTION

Sexual selection theory predicts that individuals should choose mates that provide them with direct or indirect reproductive benefits (Kirkpatrick & Ryan 1991; Andersson 1994). However, the possibilities for female choice can be severely restricted through male–male competition and sexual coercion (Qvarnström & Forsgren 1998). Here, the term sexual coercion refers to cases where males pursue, catch and restrain females and forcefully copulate with them (Clutton-Brock & Parker 1995). Factors promoting such behaviour include both phenotypic traits, such as superior speed and strength or intromittent organs in males, and ecological conditions that lead to clumped aggregations where female movements are restricted and males cannot effectively control mating access to females (Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Gowaty 1997).

Under these circumstances, selection will favour females that can reduce the probability of their offspring being sired by non-preferred males even after copulation has begun. One possibility is 'cryptic' female choice, broadly defined as a female-controlled process which selectively favours paternity by males with a particular trait over paternity of males that lack the trait when the female has copulated with both types (Eberhard 1996). Such cryptic female choice has been reported for more than 100 species (Eberhard 1996), but in many cases alternative explanations were not excluded. Hence, there is an ongoing debate about the relative importance of female-controlled sperm selection and male-controlled sperm competition in skewing paternity (reviewed by Birkhead 1998).

Whatever the precise mechanism, most of the *ca.* 20 described mechanisms of cryptic choice are feasible only in species with internal fertilization (Halliday & Verrell 1984; Jennions *et al*. 1992; Eberhard 1996; Halliday 1998). Yet, sexual coercion by males also occurs in species with external fertilization. Typical examples come from several frog and toad species in which females are often forcefully amplexed by males other than the preferred males (Halliday 1983; Bourne 1993). Can coerced females of such species nevertheless exert mate choice?

European waterfrogs of the *Rana lessonae–Rana esculenta* complex provide an excellent model system for studying this question, because in this complex mating with the 'wrong' male will result in no reproductive success at all, rather than in a small reduction in fertility as has been reported for other anuran species (Davies & Halliday 1977; Ryan 1985; Robertson 1990). This is due to a rare reproductive mode known as 'hybridogenesis' (Schultz 1969). During gametogenesis, *R. esculenta* (genotype *LR*)—which originated as an interspecific hybrid between *R. lessonae* (*LL*) and *Rana ridibunda* (*RR*) (Berger 1977)—eliminates its *L* genome and produces eggs and sperm containing only the *R* genome (Tunner 1974; Uzzell *et al*. 1980). As exclusion occurs prior to or during meiosis (Graf & Müller 1979; Uzzell *et al*. 1980; Tunner & Heppich 1981), recombination through crossing-over is normally prevented and the *R* genome is transmitted closely (for exceptions see Uzzell *et al*. (1977) and Hotz *et al*. (1992)). In areas without *R. ridibunda*, *LR* × *LR* matings (i.e. hybrid × hybrid) lead to *R. ridibunda* tadpoles, but these usually die during the larval stage or shortly after metamorphosis, both under laboratory and nearly natural conditions (Berger 1976; Semlitsch & Reyer 1992). The cause of this low viability is assumed to be an accumulation

of lethal factors on the clonally transmitted *R* genome (Berger 1976; Graf & Müller 1979; Uzzell *et al*. 1980). As a consequence, the hybrid can reproduce successfully only when it regains the lost *L* genome by mating with *R. lessonae*, its genetic host. In contrast, *R. lessonae* should avoid mating with the sexual parasite, since the resulting *R. esculenta* will again eliminate the *L* genome. Hence, in the *LL–LR* system, a sexual parasite–host conflict is superimposed on the female–male conflict which exists in all species with sexual coercion.

However, in this conflict the cost:benefit ratio from mating with *LR* individuals is likely to be more detrimental to females than to males, because the repeatedly mating males only lose some time and relatively cheap sperm whereas females may lose the reproductive potential of a whole season (Abt & Reyer 1993). Hence, the ability of females to exert choice even under coerced mating would be beneficial. Indeed, preference for *LL* mates exists in both *LL* and *LR* females, but not in males (Abt & Reyer 1993; Engeler 1994). However, female preference is overrun by male–male competition: when exposed to three different *LL:LR* ratios of interacting males, females formed amplexed pairs in proportion to the male ratio (Bergen *et al*. 1997). Yet, direct observations of amplectant pairs and analyses of clutches from ponds with known sex and genotype ratios among adults revealed that *LL* males are significantly more often involved in successful amplexi than expected under the assumption of random mating (Engeler 1994; G. Abt, personal communication; H.-U. Reyer, unpublished data). This suggests that females have some subtle means of mate choice, even when exposed to competing males and forcefully amplexed.

In this study, we investigated whether females adjust the number of eggs laid according to the genotype of their mates. This is one of the few cryptic choice mechanisms possible in species with external fertilization, but it has never been clearly demonstrated (Eberhard 1996). Our experiment was designed (i) to test for the possibility of clutch size adjustment (mating sessions A and B), (ii) to investigate the consequences of such adjustment for future reproduction within (session B) and between years (session C), and (iii) to analyse the proximate mechanisms underlying the trade-off between present clutch size adjustment and future reproduction. Although we did not allow females to choose mates (either directly or indirectly), we can infer their preferences from the occurrence of clutch size adjustment and its fitness consequences.

2. METHODS

(a) *Natural history of waterfrogs*

Waterfrogs reproduce in a wide variety of ponds, ranging from shallow ditches to small lakes. During the breeding period (May–July), males remain at ponds for several weeks and wait for the asynchronously arriving females. This results in a male-biased operational sex ratio (OSR), with severe competition between males and limited possibilities for female choice, as is typical for 'prolonged breeders' (Wells 1977). Under these conditions competitively superior males can mate with more than one female. Ranid females, in contrast, are usually assumed to mate only once per season and they may even skip a year of reproduction when their fat reserves are low and/or

environmental conditions are not suitable (Burkardt 1912; Rastogi *et al*. 1983; Sjögren 1991; Bättig 1998; G. Abt, unpublished data). Any eggs not released during one breeding season are resorbed in summer. From early September to the end of October, the newly acquired and resorbed resources are then invested in new follicles for the next breeding season (Burkardt 1912; Rastogi *et al*. 1983). This trade-off between present and future reproduction will be favoured only if females have a chance to breed again. This is true for waterfrogs: with annual survival rates of 55–80%, adult females have an expected life span of two to five breeding seasons and some individuals survive to eight years of age (Sjögren 1991; A.-K. Holenweg, unpublished data).

(b) *Experimental animals*

During May and June of 1995, 1997 and 1998, male and female frogs were caught from a natural pond at night and were immediately weighed, measured and genotyped via albumin electrophoresis of lymph taken from a small incision between two toes of a hind foot (Vogel 1973). In order to allow individual identification throughout the experiments (particularly in communal holding pens), all frogs were marked with a transponder (TROVAN ID 100, Pameda AG) introduced into their lateral lymphatic sac (Sinsch 1992). From body mass (M) and snout–vent length (SVL) we calculated female condition indices (CI) with the following equation: $CI = M \times 10\,000/(SVL)^3$ (Jørgensen 1992, p. 442). Only females with a $CI \geqslant 1.15$ were used for the experiments, because they are likely to carry eggs and be ready to spawn (H.-U. Reyer, G. Frei and C. Som, personal observations).

(c) *Mating experiments*

All experimental animals went through two mating sessions (A and B) and some also through a third one (C). The set-up for sessions A and B consisted of four identical ponds, each measuring $2.3\,m \times 4.4\,m$, equipped with three water plants and surrounded by drift fences. Video cameras mounted above the ponds recorded the position and behaviour of the frogs throughout the day and night every 10 min for 30 s.

(i) *Mating session A*

One or two days after being caught, one pair of each of the four possible mate combinations ($LL \times LL$, $LL \times LR$, $LR \times LL$ and $LR \times LR$; first letters are the female and second letters are the male) was introduced into each of the ponds. Pairs remained there for one or two days, depending on when the first spawning occurred in any of the four ponds.

(ii) *Mating session B*

Thereafter, all frogs were removed and the females moved to a new pond where each of them was matched with a male of the other type: *LL* and *LR* females which had been together with an *LL* male in session A were now exposed to an *LR* male and those females which had been together with an *LR* male were exposed to an *LL* male. For this session, which also lasted for one to two days, we used new males to eliminate the potential effects of sperm depletion (Halliday 1978; Bourne 1993).

In both session A and B, frogs were assigned randomly to mates and ponds within the female:male SVL ratio of 0.81–1.43 (mean ± s.d. 1.14 ± 0.16). Each of the four possible female–male combinations was replicated with freshly caught frogs ten times (four times in 1995, five times in 1997 and once in 1998), with all experiments occurring between 29 May and

Table 1. *Number of experiments (n) in total and broken down into cases where females produced no clutch or spawned without amplexus and with amplexus*

(The numbers are further classified by mate combinations (female × male): $LL = R.$ *lessonae* and $LR = R.$ *esculenta*. Eggs refers to the mean number of eggs per gram of body mass laid by females in the respective situations (adjusted least-square means from the MANOVA).)

mate combination	total	no clutch	without amplexus		with amplexus	
female × male	n	n	n	eggs	n	eggs
$LL \times LL$	10	1	4	7.4	5	53.5
$LL \times LR$	10	1	4	6.0	5	31.9
$LR \times LL$	10	6	1	10.5	3	71.6
$LR \times LR$	10	3	2	13.1	5	49.9
total	40	11	11	—	18	—

26 June. By putting only one pair into a pond we guaranteed that the female was amplexed by only one male which (i) mimics the usual situation in these frogs after a pair has formed, and (ii) eliminates direct male–male and sperm competition as confounding factors on measures of reproductive success. Whether or not amplexus had occurred was deduced from video surveillance and from the presence or absence of fertilized eggs in the clutch.

(iii) *Overwintering*

At the end of session B, frogs were separated by sex and genotype and transferred to communal holding pens where they remained until mid-October. In 1995 and 1998 they were then released into their pond of origin. In 1997, we kept 18 females, gradually cooled them from 15 to 5 °C over a period of one week and kept them at this hibernation temperature until 2 February 1998. Thereafter, they were rewarmed to 20 °C over ten days and exposed to day lengths increasing from 10 to 16 h within one month.

(iv) *Session C*

When the first overwintered females started releasing eggs without a male being present (12 March 1998), the others were put together with one *LL* male each in 90-l aquaria containing water plants and allowed to spawn.

(d) *Dependent variables*

In all three sessions (A–C), ponds or aquaria were regularly searched for spawn and all eggs were removed and transferred to 5-l dishpans containing aged tap water. The eggs were counted and kept for several days to check whether fertilization (and, hence, amplexus) had occurred. This post-hoc test for successful mating works with all female × male combinations, even for the *LR* × *LR* pairs, because the resulting *RR* tadpoles only die later. Adult frogs were weighed before and immediately after mating and also in autumn, 8–12 weeks after spawning. Since egg numbers in frogs increase with body size and *R. esculenta* is, on average, bigger than *R. lessonae* (Berger 1977), all clutch sizes are expressed as the number of eggs per gram of female body mass.

In early September (1–3) and mid-October (14–16) of 1997, we drew small samples of blood (10–40 µl) from an incision made between two toes of a hind foot. From these samples, plasma titres of testosterone–dehydrotestosterone, which correlate positively with next year's egg production (Licht *et al.* 1983), were analysed through radioimmunoassay. Cross-reactions were measured with the antibodies AK8/3 or AK8/5/10, which allow detection of hormone concentrations in the order of $\geqslant 1 \, \text{ng ml}^{-1}$ (based on 10 µl plasma). Details of the analysis techniques have been described elsewhere (Fenske & Probst 1982).

(e) *Statistics*

Egg numbers and the condition indices were related to the genotypes of and size ratios between females and males by means of multi- and univariate analyses of variance. Various pairwise relationships between egg numbers, body condition and hormone titres were tested through regression analyses, after controlling for confounding genotype effects where necessary. Differences were considered significant at $p \leqslant 0.05$. Data are given as means ± s.e. All analyses were performed with Systat 7.0 for Windows (SPSS Inc. 1997).

3. RESULTS

(a) *Spawning adjustment*

Out of the 40 females used in both mating sessions, 11 did not release eggs in either experiment, while the remaining 29 females spawned in either mating session A, B or both, 18 of them with and 11 without amplexus (table 1). Considering only the cases of unsuccessful reproduction, their frequencies were not related to the pair combinations for either (i) the 11 cases with no eggs, or (ii) the 11 cases with eggs but no amplexus, or (iii) all 22 cases together (all $p > 0.621$, Fisher's exact probability test, two-tailed).

A multivariate analysis of variance (MANOVA) based on the 29 cases where oviposition occurred also revealed no effect of the specific pair combination on spawning, as indicated by the non-significant values for the size ratio ($p = 0.46$) and male × female interaction ($p = 0.51$; table 2). However, the MANOVA did show that the clutch sizes depended on both female and male type (table 2). In terms of female type, the egg number per gram of body mass was 1.45 times higher for *LR* females than for *LL* females (figure 1a and table 1). In terms of male type, the clutch size increased from females spawning without being amplexed through those mating with *LR* males to those mating with *LL* males (figure 1b and table 1).

(b) *Multiple mating*

Seventeen out of the 29 spawning females released their first eggs during mating session A. Fourteen out of

Table 2. *Summary statistics of an analysis of variance based on first ovipositions (in either session A or B) of 29 females*

(Egg numbers per gram of body mass, female condition in spring (prior to spawning) and condition loss due to spawning were related to two female types (*LL* and *LR*) and three amplexus situations ('male type') (no amplexus, amplexed by an *LR* male or amplexed by an *LL* male) as well as to the interaction of female and male type and the size ratio (SVL) of the (potential) mates. The results from the multivariate model and the univariate analyses are shown, with significant p-values in bold type.)

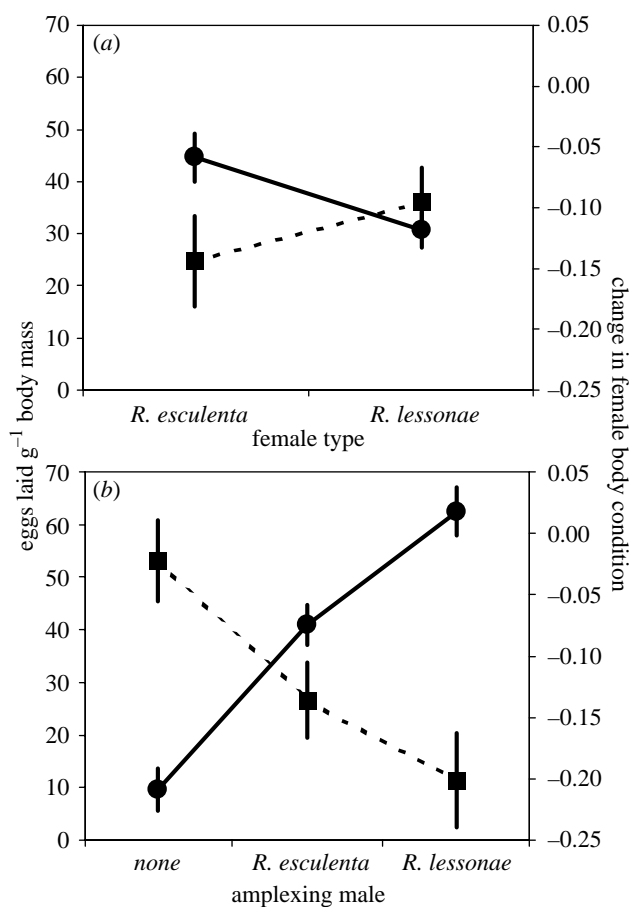|	multivariate			univariate						
	Wilks' λ			egg number			condition in spring		condition loss	
$n = 29$	d.f.	F	p	d.f.	F	p	F	p	F	p
female type	3,20	3.08	**0.05**	1,22	4.51	**0.04**	1.84	0.19	0.87	0.36
male type	6,40	8.20	**0.00**	2,22	39.45	**0.00**	0.30	0.75	7.10	**0.00**
female × male	6,40	1.52	0.20	2,22	0.70	0.51	2.76	0.09	0.49	0.62
size ratio	3,20	2.39	0.10	1,22	0.57	0.46	1.75	0.20	2.54	0.13

Figure 1. Clutch size (eggs laid per gram of female body mass) and change in female body condition due to spawning in relation to (*a*) two female genotypes and (*b*) three amplexus situations: females spawning alone and females spawning with *R. esculenta* or *R. lessonae* males. The change in body condition was calculated as the difference between the CI in mid-September (8–12 weeks after reproduction) and that immediately before reproduction. Data are given as means ± s.e. Filled circles, eggs laid; filled squares, female body condition.

these 17 females did not spawn again after mates were switched in session B, but three (17.6%) did. In two of these three cases, $LR \times LR$ matings in session A were followed by $LR \times LL$ matings in session B, with approximately equal proportions of eggs laid during both sessions
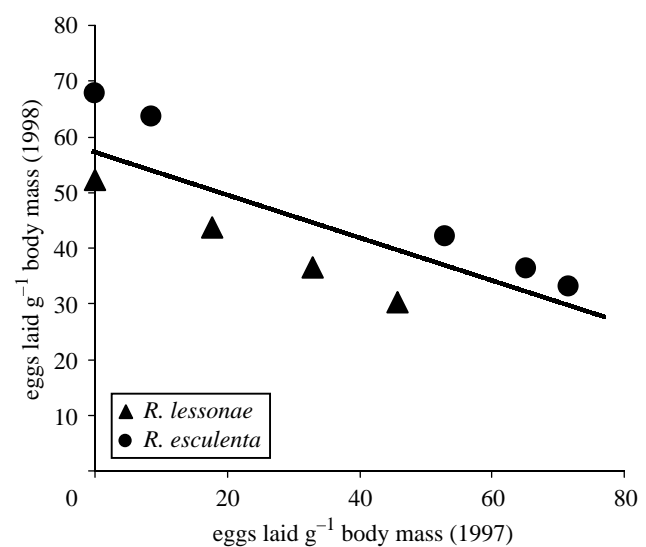

Figure 2. Relationship between clutch sizes in 1997 and 1998 for females of *R. lessonae* (triangles) and *R. esculenta* (dots). The egg numbers in 1998 are estimates obtained from an ANCOVA which simultaneously controlled for female effects (*LL* and *LR*) on clutch size (cf. table 1). Each data point represents one female that produced a clutch in 1998 while amplexed by a *R. lessonae* male. The regression line is given by the equation $y = -0.397x + 58.1$ ($r_{1,7} = 0.816$ and $p = 0.007$).

(53 versus 47% and 61 versus 39%, respectively). In the third case, an $LL \times LL$ mating in session A was followed by an $LL \times LR$ mating in session B, but this time the egg ratio between the first and second matings was 90:10%. The remaining 12 out of the 29 females did not spawn before session B and, hence, had no chance of multiple mating during the same season.

(c) *Future reproduction*

However, eggs withheld in one year increased reproductive output in the following year (session C). Out of 18 females that were held in captivity over winter, nine spawned the following year while amplexed by *LL* males. An ANCOVA ($R_{2,6}^2 = 0.721$) controlling for the effect of female type revealed a significant negative relationship ($p = 0.007$) between clutch size in 1997 and clutch size in 1998 (figure 2).
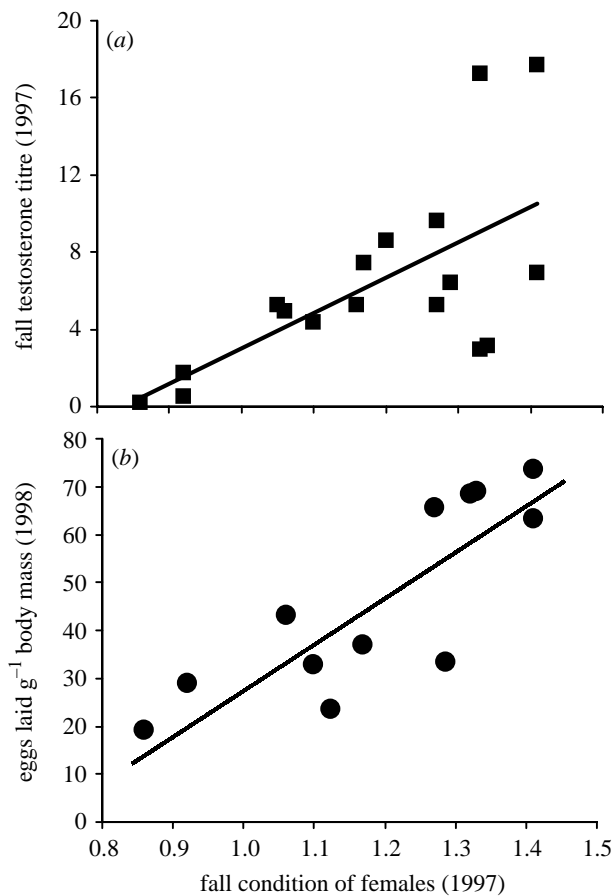
Figure 3. (*a*) Testosterone plasma titres (ng ml^{-1}) in autumn 1997 and (*b*) number of eggs spawned per gram of body weight in 1998 in relation to female condition in autumn 1997. In (*b*) the egg numbers are estimates obtained from an ANCOVA which simultaneously controlled for male and female effects on clutch size. The regression line in (*a*) is given by the equation $y = 19.1x - 16.3$ ($r_{1,16} = 0.658$ and $p = 0.003$), and the line in (*b*) by the equation $y = 99.3x - 72.6$ ($r_{1,10} = 0.837$ and $p = 0.001$).

(d) *Proximate mechanisms*

This trade-off between present and future reproduction is probably mediated through body condition. The spring condition indices before session A did not differ between females (table 2), but loss of condition after spawning reflected the previous reproductive effort: it was least in females that had spawned alone, greater in those that had mated with *LR* males and greatest in those mated with *LL* males (table 2 and figure 1). The lower the number of eggs per gram of body mass released during the breeding season, the better the body condition in early September ($CI = -0.003 \times \text{eggs} + 1.128$; $r_{1,27} = -0.456$ and $p = 0.013$). In turn, the September condition was related to the autumn hormone titres (figure 3*a*) and to the following year's reproductive output in mating session C (figure 3*b*).

4. DISCUSSION

Our experiment shows that gravid *LL* and *LR* females release some of their eggs, even when not amplexed by males, but beyond this threshold they can (and do) adjust clutch size in relation to their mate preferences. When grasped by the genetically 'undesired' *RL* males, they laid fewer eggs than when exposed to the preferred *LL* males.

Although the extent of clutch size reduction seemed to be slightly higher in *LL* (40%) than in *RL* females (30%) (table 1), the overall response did not differ between the two females types, as indicated by the lack of a significant female × male interaction (table 2). At present, we do not know whether clutch size adjustment also occurs when females are exposed to males with smaller quality differences between them (e.g. two *LL* males). However, this can be tested with a similar experimental approach, which could be further improved by comparing the reproduction of females that were or were not allowed to choose a mate.

The only other anuran for which clutch size adjustment in relation to male partners has been reported is the red-eyed treefrog (*Agalychnis callidryas*), but in this species the adjustment is not related to mate preferences: females clasped by several males lay fewer eggs than those amplexed by only one male. This probably serves to reduce egg mortality which occurs when three or more males are clinging to a female (D'Orgeix (1996) cited in Halliday (1998)).

In our waterfrogs, the reduction in the current egg output enhanced future reproductive success in two ways. One way was to produce more than one clutch within the same season. Only three out of 17 females did this, a sample too small for making any general statement about the importance of this mechanism. Better supported is the second way: improved body condition in late summer and autumn. Although our data demonstrate only correlations between clutch size in summer and body condition and plasma levels of gonadal hormones in autumn and egg numbers the following year (figures 2 and 3), evidence available from other studies strongly suggests causal relationships between these measures. The following year's reproduction is initiated from early September to the end of October; the number of vitellogenetic and mature follicles increases markedly and the ovaries grow in weight (Rastogi *et al*. 1983; Delgado *et al*. 1990). The resources for the autumn investment are drawn from food uptake, fat bodies and resorbed follicles not spawned during spring and summer (Burkardt 1912; Jørgensen 1982; Rastogi *et al*. 1983). With decreasing food supply and/or fat stores, resorption—as measured by the proportion of atretic follicles—becomes more and more important (Burkardt 1912; Rastogi *et al*. 1983). Thus, the resorption of unreleased eggs probably provides the proximate explanation for the ultimately important link between reduced oviposition in one year and improved reproduction in the next year, which has also been found in the natterjack toad *Bufo calamita* (Tejedo 1992).

In the light of this interpretation, the question arises as to why females clasped by *RL* males release eggs at all. One possible answer is that this is the only way to 'satisfy' the male and terminate the amplexus as soon as possible. Another not mutually exclusive explanation is the following: eggs remaining in the oviduct are liable to swelling when water enters through the cloaca and the resulting jelly mass can prevent subsequent oviposition or even threaten the female's life (Günther 1990). Although ovulation can be triggered through environmental factors such as temperature and rainfall, it is often enhanced through amplexus (Duellman & Trueb 1986; Jørgensen

1992). This may explain why the number of eggs released from the oviduct is higher in females clasped by *RL* males than in those not amplexed at all.

Our study does not identify the particular cues used by females to distinguish between *LL* and *LR* males. However, given the definition of cryptic female choice in § 1, knowledge of these cues is not essential and, in fact, is also lacking in many studies of overt, i.e. pre-copulatory, female choice (summarized by Andersson 1994). Any cue from mating that originates in the male and is used by the female to favour selectively paternity by males which provide better stimulation than others could be subject to sexual selection (Eberhard 1996). Possible mechanisms include differences between males in behaviour during copulation, such as calling (Licht 1969; Price & Meyer 1979), tapping, kicking, rubbing, squeezing and pressing the female (Rabb & Rabb 1960; Salthe & Mecham 1974), presenting her with nuptial gifts (Thornhill 1983; Sakaluk 1997) or stimulating her with secretions from specific glands (Duellman & Trueb 1986) or through genital movements. Several of these mechanisms—some of which also occur in anurans—have been found to influence the duration of copulation, transport of sperm to the fertilization sites, ovulation, egg maturation, the oviposition rate and other processes potentially linking female reproduction to male quality (for an extensive review see Eberhard (1996)).

From a functional point of view, the female choice mechanism found in this study may be particularly important in waterfrog matings with their marked consequences on fertility, but the implications of our results go beyond this and the few similar systems reviewed by Dawley & Bogart (1989). The ability to adjust clutch size in response to male quality allows females to exert preferences, even when sexually coerced. Such adjustment would be beneficial in all cases where interbreeding between species, ecotypes, populations, families or other groups with differences in genetic compatibility leads to lower fitness than within-group matings. Moreover, our study questions the common notion that cryptic choice can only be exercized if a female copulates with more than one male during any given fertile period (Eberhard 1996). Our finding that clutch reduction in relation to the copulatory partner of one year improves the residual reproductive value through larger clutches in the next season suggests that sexual selection on cryptic choice can operate, even in seasonally monandrous species.

Thus, female choice through clutch size adjustment may be an underestimated mechanism in species with external—and perhaps also internal—fertilization. Potential candidates for investigating this mechanism include all species with large variations in clutch size, particularly those with male coercion.

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