

Male adaptive stupidity: male mating pattern in hybridogenetic frogs

Dirk Sven Schmeller,^{1*} Robert O'Hara² and Hanna Kokko³

¹*Ecologie des Hydrosystèmes Fluviaux, Université Claude Bernard, Bât Darwin C, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France,*

²*Department of Mathematics and Statistics and* ³*Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, University of Helsinki, FIN-00014 Helsinki, Finland*

ABSTRACT

Question: Why do male frogs invest in heterospecific matings in hybridogenetic systems with large heterospecific and small conspecific females? When is a strategy to mate with larger females evolutionarily stable?

Mathematical method: A continuous-time model of reproductive values with discrete classes of individuals is developed to investigate the balance between two strong selective pressures: large conspecific females are the best mates, but large females are also more likely to be heterospecific.

Key assumption: Males can detect female size, but are unable to distinguish between conspecific and heterospecific females. Matings incur time costs and the mating season is limited. Therefore, males of the small parental species should evolve to ignore heterospecific females.

Conclusion: The results indicate that direct benefits of male mate choice within conspecifics can counteract the selective pressure to avoid large females as mates. This trade-off can balance out in a way that makes indiscriminate mating adaptive.

Keywords: adaptive decision, hybridogenesis, interspecies conflict, mating behaviour, mating strategy.

INTRODUCTION

Males of numerous species have to compete for access to females and, given the small cost involved in fertilizing a female's eggs, males are typically seen as the non-choosy sex (Andersson, 1994). However, exceptions regularly occur, and even relatively small costs of mating can lead to male mate choice (Kokko and Monaghan, 2001). A central prerequisite for this is sufficient variation in female quality as a mate (Owens and Thompson, 1994; Kokko and Monaghan, 2001; Pelabon *et al.*, 2003). In some species, females have evolved signals to attract males (e.g. Berglund and Rosenqvist,

* Author to whom all correspondence should be addressed. e-mail: dirk@die-schmellers.de
Consult the copyright statement on the inside front cover for non-commercial copying policies.

2001; Domb and Pagel, 2001; Nunn *et al.*, 2001; Pilastro *et al.*, 2003), but in many reptiles, amphibians and fish, male preferences simply focus on female size (e.g. Pettus and Angleton, 1967; Berven, 1981; Shine *et al.*, 1996; Pelabon *et al.*, 2003).

In anurans, a preference for large females is only limited by mechanistic limitations on body size, as a small male may not be able to fertilize the majority of eggs released by a female who is too large (e.g. Davies and Halliday, 1977; Ryan, 1985; Robertson, 1990). However, mating with a larger female will still confer a higher reproductive value due to the female's higher fecundity (Blankenhorn, 1977; Lada *et al.*, 1995), as well as clear carry-over effects to adulthood. Empirical studies of several species have demonstrated that a large size at metamorphosis is related to egg size, and results in higher survival, fecundity and growth rates in later life stages (Smith, 1987; Goater, 1994; Räsänen *et al.*, 2003).

Selective pressure can lead to a preference for small females. This arises if a preference for large females leads to heterospecific matings, with zero fitness gain (e.g. Pfennig, 2003). Such erroneous matings based on preferences for fertility indicators occur in males of the fishes *Poecilia mexicana* and *P. latipinna*. Males of these two species prefer to mate with larger, but gynogenetic, females of *P. formosa* (Schlupp and Ryan, 1996). Similarly in frogs, males mate repeatedly with females without regard for the species; for example, *Rana lessonae* males will mate with *R. ridibunda* females and produce *R. kl. esculenta* hybrid offspring (Abt and Reyer, 1993; Hellriegel and Reyer, 2000; Roesli and Reyer, 2000; Engeler and Reyer, 2001). In both systems, males of the smaller parental species will try to mate with females of larger size, following a 'bigger is better' strategy (Blankenhorn, 1977; Lada *et al.*, 1995). These females may not be conspecific to the males, so matings will usually lead to hybrid offspring. Intuitively, the presence of both conspecific and heterospecific (including hybrid) females might exert strong selective pressure on males, leading to a preference for small females. These small females are more likely to be conspecific, but have substantially lower fecundities compared with heterospecific females. The interspecies conflict over mating should select for a high degree of assortative mating within parental species (Hellriegel and Reyer, 2000). Hybridization-impeding behaviour, however, may also persist if both the probability of mating with a non-conspecific female and the fitness cost of such matings are both low (Pfennig, 1998, 2000).

The present theoretical study examines male mating strategies in a frog complex, characterized by hybridogenesis (Fig. 1). The complex comprises three hybridogenetic systems, which are geographically separated. Each system consists of the largest European frog species *R. ridibunda*, a small parental species (*R. perezi*, *R. lessonae* or *R. bergeri*) and their medium-sized hybrids (*R. kl. grafi*, *R. kl. esculenta* or *R. kl. hispanica*, respectively). In these hybrids, hybridogenetic gametogenesis prevents mispairings of non-homologues. This is achieved by the exclusion of the small species genome before meiosis, which is therefore lost for reproduction. The remaining genome of the large species is endoreduplicated by cloning, allowing a normal meiosis, which leaves the hybrids fully fertile. Backcrosses between the small parental species and the hybrid maintain the hybrid lineage (secondary hybrids), while matings between the parental species lead to fertile, primary hybrids; genetically these two hybrid types are indistinguishable. In frog assemblages, the offspring from matings with large females will be fertile hybrids (both primary and secondary), reproductively mimicking the larger parental species due to hybridogenesis. These hybrids do not contribute to the small parent's fitness (Fig. 1).

We address the problem of finding mating conditions under which a 'bigger is better' mating strategy is still selectively advantageous, even if reproductive potential is lost by matings with heterospecific females. Why should males of the smaller parental species not

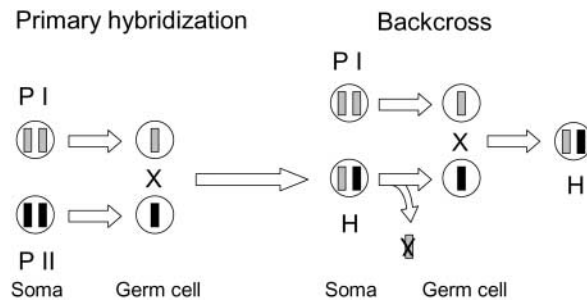


Fig. 1. Hybridogenesis. A primary hybridization of two parental species PI and PII results in a hybridogenetic hybrid (H). During gametogenesis, the hybrid H excludes the genome of the parental species PI and passes the maternal genome of the second parental species PII to the next generation (Tunner, 1970). To maintain its lineage, H backcrosses with PI to regain the excluded genome.

evolve to avoid matings, which do not produce individuals of their own species? The results from our mathematical model suggest that a direct benefit of male mate choice within conspecifics can counteract the selective pressure to avoid large females as mates. This trade-off typically balances out in a way that makes indiscriminate mating adaptive.

THE MODEL

We assume that males can detect female size, but are unable to distinguish between conspecific (small species) and heterospecific (hybrid and/or large species) females. The environment of matings is described by the abundance of conspecifics and heterospecifics, the body size distribution of conspecific and heterospecific females, the variance in body size, the mortality rate in different mating states, and the duration of mating. For simplicity, we assume that they gain no fitness at all from matings with the hybridogen or *R. ridibunda* females, as the progeny from these matings are of a hybrid kind (see Introduction). This makes the model conservative: if we can explain matings even though there is no fitness gain, then any such gain from heterospecific matings would strengthen the reason for males to mate with them.

We assume that a male can be in three states: single (denoted 0), spawning with a conspecific female (C), or spawning with a heterospecific female (H, which can either be the hybrid or *R. ridibunda*). These states can occur repeatedly, thus we take into account that a male who mates with a heterospecific female may not incur high fitness costs: he can also mate with a number of conspecifics afterwards. Such a behaviour appears to be common among anurans, as reports of multiple matings are numerous for a range of anuran genera (e.g. Seppä and Laurila, 1999; Byrne and Roberts, 2000; Vieites, 2003). During spawning with a conspecific, the male gains fitness at a rate equal to the female's size. In other spawnings, the male gains nothing. The average time it takes to spawn is T , and it is exponentially distributed (see, for example, Härdling and Kaitala 2005). The size of conspecific females is normally distributed with mean s_C and standard deviation σ_C . Heterospecific females have mean s_H and standard deviation σ_H . A single (non-spawning) male encounters conspecifics at a rate e_C and heterospecifics at a rate e_H . The mortality rate of a male is μ_0 when single and μ while spawning (Fig. 2). Although differences in mortality between the different stages are likely to be great, no empirical data have been collected. We deduce this hypothesis from behavioural

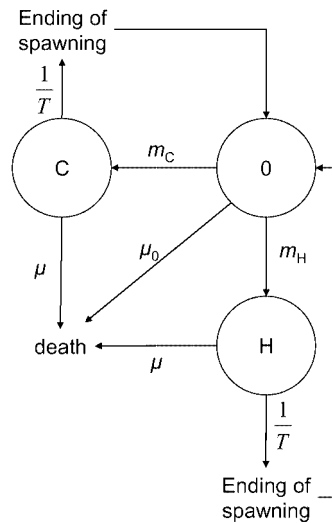


Fig. 2. The flow diagram describing possible state transitions in the model: from single (0) to spawning with heterospecific (H) females or with conspecific (C) females; ending of spawning ($1/T$), and death. This flow diagram forms the basis of equation (1).

observations. While single males are extremely active, fighting for territory, calling in choruses and swimming around seeking females, the mortality rate is substantially higher due to risk of predation such as during amplexus (mating). During amplexus, males stop calling, and remain unobtrusive, while the female seeks a suitable spawning location, usually avoiding open waters (Günther, 1990; D.S. Schmeller, personal observation).

We next derive the equations for changes in male fitness, assuming that a male can decide to mate with any female, or have a preference for large females (rejecting any that fall below a threshold X_S) or for small females (rejecting those whose size exceeds a threshold X_L). We use a method described in detail by Härdling *et al.* (2003), which assumes a continuous-time model with discrete classes of individuals, who obey certain transition rates from one (discrete) stage to the other. Only one of the states, spawning with a conspecific female, gives the male an immediate fitness gain. This gain occurs at a rate that depends on the size of the female, and the accumulation of fitness stops when the mating is completed. Fitness in other states depends on the rates of eventually entering the reproductive state. All rates can be summarized in a flow diagram (Fig. 2), which can be expressed as a transition matrix that expresses continuous rates of moving from one state to another. For a more detailed mathematical derivation of this technique that allows an analysis of continuous-time models in matrix form, see Härdling *et al.* (2003). The reproductive value equation is

$$\begin{pmatrix} \frac{dv_0}{dt} \\ \frac{dv_C}{dt} \\ \frac{dv_H}{dt} \end{pmatrix} = \begin{pmatrix} -(m_C + m_H) - \mu_0 & m_C & m_H \\ \frac{1}{T} & -\frac{1}{T} - \mu & 0 \\ \frac{1}{T} & 0 & -\frac{1}{T} - \mu \end{pmatrix} \begin{pmatrix} v_0 \\ v_C \\ v_H \end{pmatrix} + \begin{pmatrix} 0 \\ \bar{s}_C \\ 0 \end{pmatrix} \quad (1)$$

Here, v_0 , v_C and v_H are the reproductive values of males of each state. The elements of the matrix are derived as follows. First, consider a single (i.e. non-mating) male. He is currently gaining no fitness, and his reproductive value v_0 therefore depends on how often he changes to states C (spawning with a conspecific female, rate m_C) or H (spawning with a heterospecific female, rate m_H). He may experience three different transitions: (i) begin spawning with a conspecific female (gain reproductive value v_C , lose v_0), (ii) begin spawning with a heterospecific female (gain v_H , lose v_0), or (iii) die (gain nothing, lose all current reproductive value). These gains and losses are tabulated in the first row of the matrix in equation (1), and they occur at rates m_C , m_H and μ_0 , respectively. The matrix multiplication takes care of the proper fitness gains and losses. For example, the rate of conspecific mating is m_C , yielding a gain proportional to $m_C v_C$ for an infinitesimally long time unit, and a loss $-m_C v_0$. These values arise from the matrix multiplication in equation (1).

The second and third rows of the matrix describe mating males. If the female is conspecific, a male mating with her gains fitness at a rate proportional to the size of the females he mates with, \bar{s}_C . If the female is heterospecific, however, the rate of fitness gain is 0. The spawning male gains fitness until he ends spawning (rate $1/T$) or dies (rate μ). If a male ends spawning, he is back at the reproductive value of a single male. The ultimate fitness of a male can be found by setting $dv_0/dt = dv_H/dt = dv_C/dt = 0$ (see Härdling *et al.*, 2003) and solving for v_0 . This gives us

$$v_0 = \frac{m_C T \bar{s}_C}{\mu_0 + (m_C + m_H + \mu) \mu T} \quad (2)$$

The acceptance threshold that a male uses for female size will influence both the mating rates m_C and m_H and the expected size of conspecific females the male mates with, \bar{s}_C . Both thresholds (X_L and X_S) have to be evaluated to find the optimal strategy. Either can model indiscriminate mating if, for example, the X_S threshold is set so high that all females in the population fall below X_S . If males accept females above a threshold X_L , the variables get the values

$$m_H = e_H \int_{X_L}^{\infty} f_H(s) ds \quad m_C = e_C \int_{X_L}^{\infty} f_C(s) ds \quad \bar{s}_C = \frac{\int_{X_L}^{\infty} s f_C(s) dx}{\int_{X_L}^{\infty} f_C(s) dx}$$

and if they prefer small females,

$$m_H = e_H \int_{-\infty}^{X_S} f_H(s) ds \quad m_C = e_C \int_{-\infty}^{X_S} f_C(s) ds \quad \bar{s}_C = \frac{\int_{-\infty}^{X_S} s f_C(s) ds}{\int_{-\infty}^{X_S} f_C(s) ds}$$

where $f_H(s)$ and $f_C(s)$ are the probability distribution functions of the size of the heterospecific and conspecific females. Both are normal distributions, so that \bar{s}_C is the expected value of a truncated normal distribution. To find the optimal behaviour of a male, we simply find the optimal values of X_S and X_L that maximize equation (2), and choose the one (X_S or X_L) that yields the higher fitness to describe optimal male behaviour.

RESULTS

When the size distribution of adult females shows almost no overlap, the optimal male strategy is size assortative mating that favours small females, and consequently leads to matings between conspecifics (Fig. 3A). Males accept any female in the size range of conspecifics and in the scenario in Fig. 3A, 100% of conspecific and 2% of heterospecific females will be accepted. In a second example with a wider variance of conspecific sizes and a narrower variance of heterospecific size, but other parameters the same, the male mating strategy shifts to indiscriminate behaviour (Fig. 3B): now any female is accepted as a mate. Note that the model can produce indiscriminate mating despite the assumption of a size threshold, since indiscriminate mating as in Fig. 3B can be, technically speaking, equated with a preference for large females with a size threshold of 0.

In some cases, a true preference for large females can evolve even if it means that the smallest conspecific females are rejected, while all heterospecific females are accepted. This can happen if the conspecific females have highly variable body sizes (Fig. 4, region with standard deviation >13): the benefits gained through a preference for large females then override the time cost of mating with heterospecifics. In this case, very few females are rejected, and the situation can almost be classified as indiscriminate mating.

The overlap in female body size distributions seems to be the most important factor determining male mating behaviour (Fig. 4). With a decreasing mean size difference and increasing standard deviation of conspecific females, the mating behaviour gradually changes from size-assortative mating (discriminating against large females) to indiscriminate mating behaviour (Figs. 4, 5D).

Males are particularly likely to accept heterospecific females as mates if the mating time is short (Fig. 5A), conspecific females are more common than heterospecific females (Fig. 5B), males are generally short-lived (Fig. 5C) and conspecific females are large (Fig. 5D). In all cases, indiscriminate mating becomes more likely with increasing variation in the body size

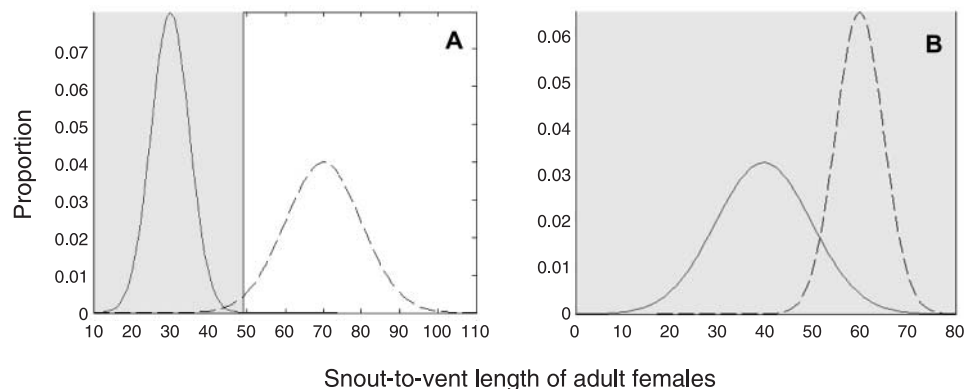


Fig. 3. Two examples of female body size distributions and the resulting male mating strategy. In both (A) and (B), conspecific females (solid line) are on average smaller than heterospecifics (dashed line), but the overlap between distributions is less in (A) than in (B). The shaded area indicates females that are accepted as mates by males. In (A), males use a size threshold above which they refuse to mate with a female. In (B), males mate with any female. Parameter values used to create the examples: in (A), $s_C = 30$, $\sigma_C = 5$, $s_H = 70$, $\sigma_H = 10$, $e_C = e_H = 1$, $\mu_0 = \mu_1 = 0.1$, $T = 0.1$; in (B), $s_C = 40$, $\sigma_C = 10$, $s_H = 60$, $\sigma_H = 5$, $e_C = e_H = 1$, $\mu_0 = \mu_1 = 0.1$, $T = 0.1$.

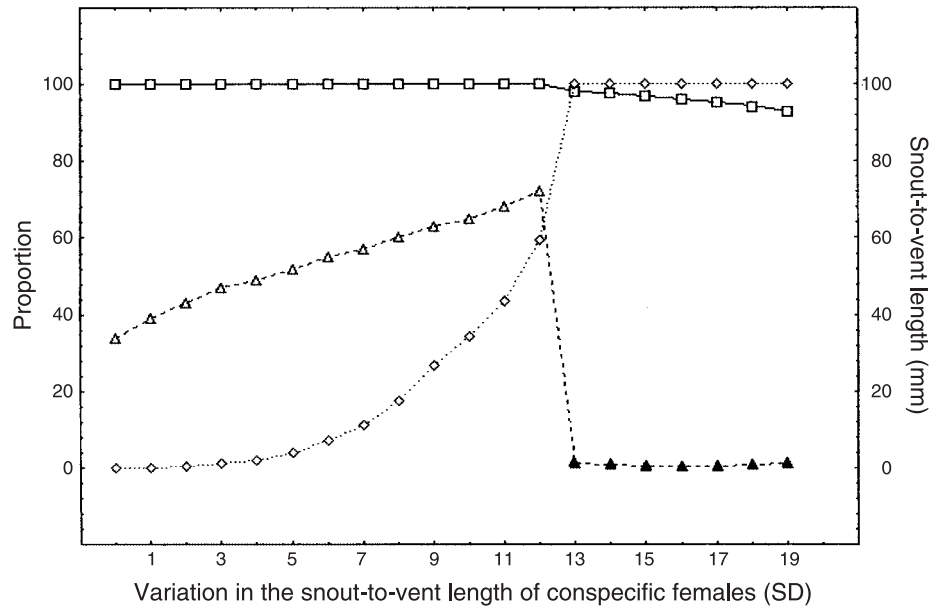


Fig. 4. The mating strategy used by males as a function of the variance in body size of conspecific females. \triangle : the upper size threshold used by males, illustrating size assortative mating. \blacktriangle : the lower size threshold used by males, illustrating indiscriminate mating behaviour. \square : the proportion of conspecific females that males accept as a consequence of the size threshold rule. \diamond : the proportion of heterospecific females that males accept. Increasing the standard deviation (SD) in conspecific snout-to-vent length first leads to an increasing size threshold that accepts small females as mates. At the largest standard deviations, the strategy changes to completely indiscriminate mating, and then to a steady decline in the number of conspecifics accepted as mates, as males begin to use a rule that favours large females despite the risk of heterospecific matings. Parameter values used: $s_C = 30$, $\sigma_C = x$, $s_H = 70$, $\sigma_H = 10$, $e_C = e_H = 1$, $\mu_0 = \mu_1 = 0.1$, $T = 0.2$.

of conspecific females (Fig. 5A–D). A change of the function of body size to fitness reveals qualitatively the same results.

DISCUSSION

Despite frequent hybridizations in hybridogenetic systems of the western Palearctic waterfrog complex, males of the smaller parental species should evolve recognition cues for conspecific females to avoid investing in heterospecific no-gain matings. However, the evolution of discrimination may be extremely difficult if the most obvious cue present (body size) conflicts with fitness benefits gained when discriminating between conspecific females of varying fecundity. Here we show that a ‘bigger is better’ strategy can lead to indiscriminate or almost indiscriminate male mating behaviour under a wide range of conditions. This is crucial for the persistence of hybridogenesis, as heterospecific matings either between two parental species or the smaller parental species and a hybrid have to occur. Both models predict that mating strategies may not prevent heterospecific matings from being adaptive, and that the frequencies of heterospecific matings under natural conditions can be large without causing selection pressure to discriminate against the largest females.

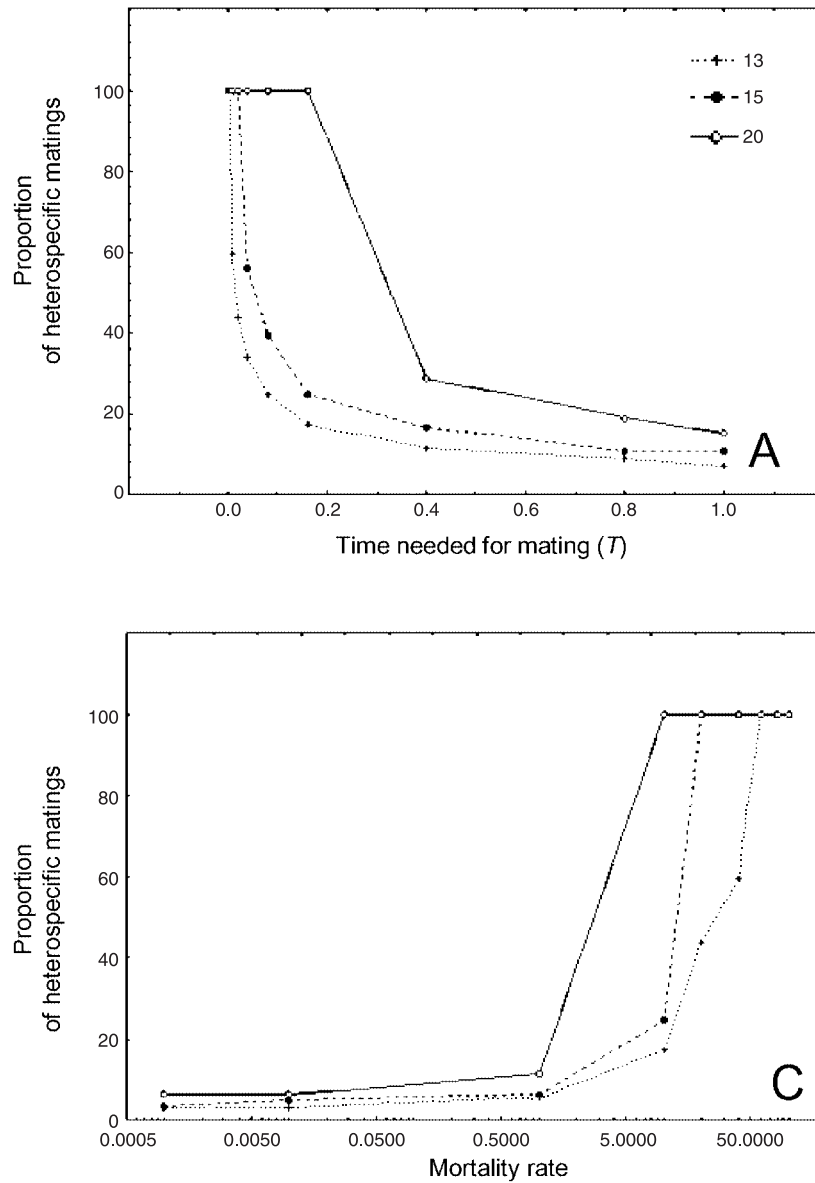
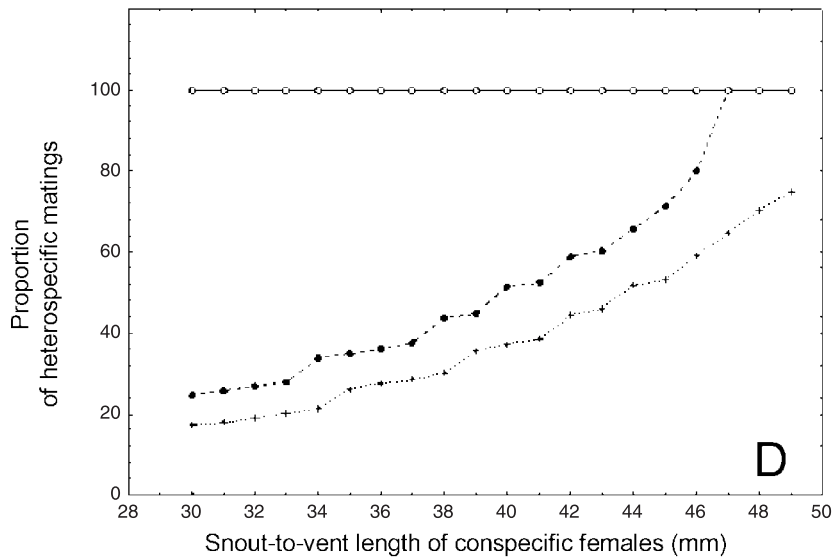
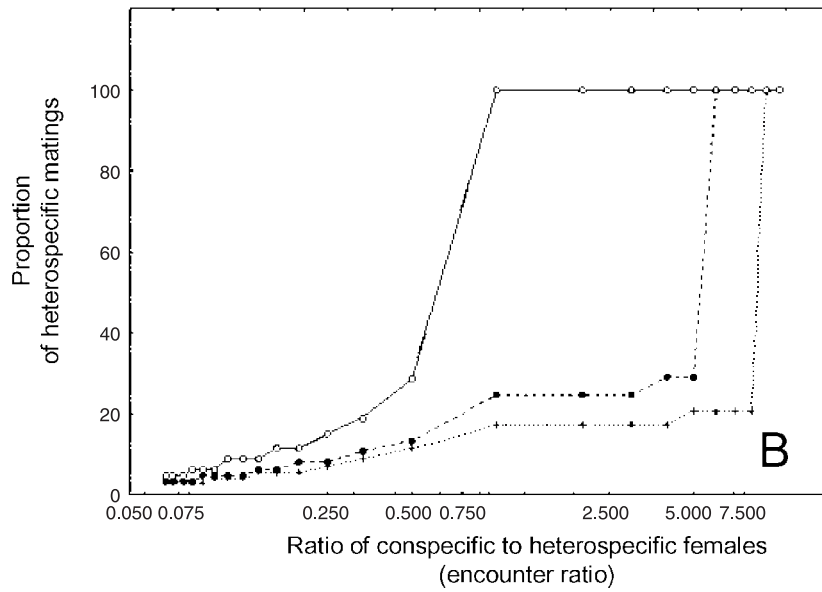


Fig. 5. Effects of: (A) time cost of mating (T); (B) proportion of conspecific females out of all females, as indicated by encounter rates; (C) male mortality rate; and (D) mean snout-to-vent (SVL) of conspecific females on the male mating strategy, indicated as the proportion of heterospecific

Our multiple mating model shows that one of the basic factors predicting the mating behaviour is the variance in body size of conspecific females. If there is an overlap between the body sizes of conspecific and heterospecific females, it may pay for a male to accept either type, even though this activity bears some costs: time wasted in no-gain matings



females the male accepts to mate with. Crosses indicate SVL variance given by the standard deviations in conspecific females of 13, 15 and 20, respectively. Parameter values used were not varied in the figure: $s_C = 20$, $\sigma_C = 13, 15$ or 20 , $s_H = 70$, $\sigma_H = 10$, $e_C = e_H = 1$, $\mu_0 = \mu_1 = 0.1$, $T = 0.2$.

implies an opportunity cost of not mating with conspecific females during this time, and a potential mortality cost if the male has no time to locate another conspecific before he dies. Importantly, lack of discrimination is often predicted by our model, even though we did not assume any cost of developing the cognitive machinery involved in discrimination. Thus,

such costs are not necessary to explain apparently maladaptive failures in cognitive tasks: the mating system itself may render discrimination unprofitable. Naturally, if cognitive costs were included in the model, indiscriminate mating would become more likely, thus strengthening our conclusion that ‘stupidity’ may be adaptive.

It is not surprising that indiscriminate mating is favoured when the time needed to mate is short. Sexual selection theory predicts a lack of choosiness when the cost of each breeding attempt is small, even if potential mates differ widely in the fitness prospects they offer (Kokko and Monaghan, 2001). Another factor that strongly favours indiscriminate mating is a high proportion of conspecific females in the population. Intuitively, it is clear that it is not worth trying to avoid mistakes that occur rarely anyway – hence, the lack of discrimination when heterospecific females are rare. It is perhaps less intuitively clear that males become less discriminating when their mortality rate is high; one might think that mate choice has to be more considered when there are only a few mating opportunities before death. However, the opposite appears to be true: males that are ‘in a hurry’ might not encounter any other female at all, and they will have to gamble and mate in the hope that the current female offers some fitness benefit. This result highlights the importance of viewing the fitness consequences in the proper dynamical context: it is not only the current activity that matters, but also what happens, in a life-history context, to a male who makes the alternative decision of not mating.

In general, if there is a size overlap then size-assortative mating does not rule out heterospecific matings. Perfect discrimination will only occur with non-overlapping size distributions of adult females. In wild populations, this is unlikely to be the case, hence assortative mating using size as a cue to distinguish between conspecific and heterospecific females would lead to a failure to mate with large conspecific females. These represent the most valuable females for these males. Being indiscriminate, therefore, may be an adaptive behaviour that reflects an underlying preference for highly fecund females, rather than ‘stupidity’ or a failure to evolve an appropriate response to body size. In other words, waterfrog males can be luckily stupid and thereby showing an adaptive behaviour. Strategic male mate choice can, therefore, be reflected in indiscriminate mating in a way that strongly contributes to the persistence of hybridogenetic population systems.

ACKNOWLEDGEMENTS

The study was supported financially by the Academy of Finland and the KONE Foundation (to D.S.S.). Many thanks to Peter Taylor for helpful comments.

REFERENCES

- Abt, G. and Reyer, H.-U. 1993. Mate choice and fitness in a hybrid frog: *Rana esculenta* females prefer *Rana lessonae* males over their own. *Behav. Ecol. Sociobiol.*, **32**: 221–228.
- Andersson, M.B. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Berglund, A. and Rosenqvist, G. 2001. Male pipefish prefer dominant over attractive females. *Behav. Ecol.*, **12**: 402–406.
- Berven, K.A. 1981. Mate choice in the wood frog, *Rana sylvatica*. *Evolution*, **35**: 707–722.
- Blankenhorn, H.J. 1977. Reproduction and mating behavior in *Rana lessonae*–*Rana esculenta* mixed populations. In *The Reproductive Biology of Amphibians* (D.H. Taylor and S.I. Guttman, eds.), pp. 389–410. New York: Plenum Press.

- Byrne, P.G. and Roberts, J.D. 2000. Simultaneous mating with multiple males reduces fertilization success in the myobatrachid frog *Crinia georgiana*. *Proc. R. Soc. Lond. B*, **264**: 95–98.
- Davies, N.B. and Halliday, T.R. 1977. Optimal mate selection in the toad *Bufo bufo*. *Nature*, **269**: 56–58.
- Domb, L.G. and Pagel, M. 2001. Sexual swellings advertise female quality in wild baboons. *Nature*, **410**: 204–206.
- Engeler, B. and Reyer, H.-U. 2001. Choosy females and indiscriminate males: mate choice in mixed populations of sexual and hybridogenetic water frogs (*Rana lessonae*, *R. esculenta*). *Behav. Ecol.*, **12**: 600–606.
- Goater, C.P. 1994. Growth and survival of postmetamorphic toads – interactions among larval history, density, and parasitism. *Ecology*, **75**: 2264–2274.
- Günther, R. 1990. *Die Wasserfrösche Europas (Anura – Froschlurche)*. Wittenberg Lutherstadt: Die Neue Brehm-Bücherei.
- Härdling, R. and Kaitala, A. 2005. The evolution of repeated mating under sexual conflict. *J. Evol. Biol.*, **18**: 106–115.
- Härdling, R., Kokko, H. and Arnold, K.E. 2003. Dynamics of the caring family. *Am. Nat.*, **161**: 395–412.
- Hellriegel, B. and Reyer, H.-U. 2000. Factors influencing the composition of mixed populations of a hemiclinal hybrid and its sexual host. *J. Evol. Biol.*, **13**: 908–918.
- Kokko, H. and Monaghan, P. 2001. Predicting the direction of sexual selection. *Ecol. Lett.*, **4**: 159–165.
- Lada, G.A., Borkin, L.J. and Vinogradov, A.E. 1995. Distribution, population systems and reproductive behavior of green frogs (hybridogenetic *Rana esculenta* complex) in the Central Chernozem Territory of Russia. *Rus. J. Herp.*, **2**: 46–57.
- Nunn, C.L., van Schaik, C.P. and Zinner, D. 2001. Do exaggerated sexual swellings function in female mating competition in primates? A comparative test of the reliable indicator hypothesis. *Behav. Ecol.*, **12**: 646–654.
- Owens, I.P.F. and Thompson, D.B.A. 1994. Sex-differences, sex-ratios and sex-roles. *Proc. R. Soc. Lond. B*, **258**: 93–99.
- Pelabon, C., Borg, A.A., Bjelvenmark, J., Forsgren, E., Barber, I. and Amundsen, T. 2003. Do male two-spotted gobies prefer large fecund females? *Behav. Ecol.*, **14**: 787–792.
- Pettus, D. and Angleton, G.M. 1967. Comparative reproductive biology of montane and piedmont chorus frogs. *Evolution*, **21**: 500–507.
- Pfennig, K.S. 1998. The evolution of mate choice and the potential for conflict between species and mate-quality recognition. *Proc. R. Soc. Lond. B*, **265**: 1743–1748.
- Pfennig, K.S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav. Ecol.*, **11**: 220–227.
- Pfennig, K.S. 2003. A test of alternative hypotheses for the evolution of reproductive isolation between spadefoot toads: support for the reinforcement hypothesis. *Evolution*, **57**: 2842–2851.
- Pilastro, A., Griggio, M. and Matessi, G. 2003. Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment? *Anim. Behav.*, **66**: 265–271.
- Räsänen, K., Laurila, A. and Merilä, J. 2003. Carry-over effects of embryonic acid conditions on development and growth of *Rana temporaria* tadpoles. *Freshw. Biol.*, **47**: 19–30.
- Robertson, J.G.M. 1990. Female choice increases fertilization success in the Australian frog, *Uperoleia laevis*. *Anim. Behav.*, **39**: 639–645.
- Roesli, M. and Reyer, H.-U. 2000. Male vocalisation and female choice in the hybridogenetic *Rana lessonae*/*R. esculenta* complex. *Anim. Behav.*, **60**: 745–755.
- Ryan, M.J. 1985. *The túngara Frog: A Study in Sexual Selection and Communication*. Chicago, IL: University of Chicago Press.
- Schlupp, I. and Ryan, M.J. 1996. Mixed-species shoals and the maintenance of a sexual–asexual mating system in mollies. *Anim. Behav.*, **52**: 885–890.

- Seppä, P. and Laurila, A. 1999. Genetic structure of island populations of the anurans *Rana temporaria* and *Bufo bufo*. *Heredity*, **82**: 309.
- Shine, R., Branch, W.R., Harlow, P.S. and Webb, J.K. 1996. Sexual dimorphism, reproductive biology, and food habits of two species of African filesnakes (*Mehelya*, Colubridae). *J. Zool.*, **240**: 327–340.
- Smith, D.C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology*, **68**: 344–350.
- Turner, H.G. 1970. Das Serumeiweißbild der einheimischen Wasserfrösche und der Hybridcharakter von *Rana esculenta*. *Verh. Dt. Zool. Ges.*, **64**: 352–358.
- Vieites, D.R. 2003. Temporal and spatial dynamics of a high mountain metapopulation of *Rana temporaria*. PhD thesis, Department of Ecology and Animal Biology, University of Vigo.