

Sequential mate choice by multiply mating smooth newts: females become more choosy

Caitlin R. Gabor^a and Tim R. Halliday^b

^aDepartment of Biology, University of Southwestern Louisiana, Lafayette, LA 70504, USA, and

^bDepartment of Biology, The Open University, Milton Keynes, MK7 6AA, England

In some species, females sequentially mate with different males within a single mating period, store sperm until the eggs are eventually fertilized, and gain no other resources from the males. Halliday hypothesized that, for such species, a female could ensure fertilization of her eggs by mating with the first male that she encounters; thereafter, she can maximize the quality of her progeny by sampling further males and by mating only with males of higher quality than previously mated males. This hypothesis predicts that females' choosiness will increase as the breeding season progresses. We tested this prediction of Halliday's hypothesis by examining mate choice by female smooth newts (*Triturus vulgaris vulgaris*). Males of this species develop a dorsal crest during the courtship season. Crest height varies between males and is potentially an indicator of male quality. Initially, female smooth newts were equally willing to mate with males with low or high crests. However, in their second mating, females remated only with high-crested males. These results support our prediction and are consistent with Halliday's hypothesis. If crest height in smooth newts is an indicator of quality, this change in females' mate choice criterion allows females both to initiate egg-laying very early in the season and, subsequently, to mate preferentially with higher quality mates. **Key words:** female choice, multiple mating, sequential mate choice, sexual selection, smooth newts, *Triturus vulgaris*. [*Behav Ecol* 8:162–166 (1997)]

Female mate choice (Andersson, 1986; Bakker and Milinski, 1991; Collins, 1995; Green, 1991; Knapp and Kovach, 1991) and multiple matings by females have been shown in many organisms including salamanders, birds, primates, and invertebrates (Halliday and Verrell, 1984; Sims et al., 1989; Small, 1992; Walker, 1980). However, few (but see Davies, 1992) of these studies address questions about the role of sequential mate choice in species where females mate multiply, foster sperm competition, and gain no other resources from males. Such questions include (1) why do females mate with more than one male? (2) what rules do females follow when choosing successive mates, and (3) do females that mate multiply use the same mate choice criteria during successive mating?

Halliday and Arnold (1987) suggested nine reasons why females may mate multiply, and many models of female mate choice tactics in sequentially mating species have been proposed (Brown, 1981; Janetos, 1980; Janetos and Cole, 1981; see review in Real, 1990; Wittenberger, 1983). In several species, females sequentially visit several males before mating (Arak, 1988; Bakker and Milinski, 1991; Dale et al., 1990, 1992; Ryan, 1985), but in these species, females mate only once in a breeding season and in all but one species females gain resources from males. Females often can visit only one male at a time, yet experimental evidence of female mate choice often comes from simultaneous choice tests in which the females' preference for association is recorded but actual matings are not observed. Choosing mates from sequentially visited males may be more difficult for a female and requires the ability to remember previously visited males for making comparisons (Bakker and Milinski, 1991; Real, 1990).

We know of only one model (Crowley et al., 1991) that addresses the problem of sequential mate choice tactics by multiply mating females: Females should prefer to mate with higher-quality males until the end of the season (or end of life span) when positive assortative mating should occur. In

addition, Halliday (1983) hypothesized that for species that mate multiply and have last male sperm precedence, a female could ensure fertilization of her eggs by mating with the first male that she encounters; thereafter, she can maximize the quality of her progeny by sampling further males and by mating only with males of higher quality than previously mated males. We know of no experimental studies that have focused on the sequential mate choice of females that mate multiply, breed in more than one mating season, and do not gain resources from males.

Smooth newts (*Triturus v. vulgaris*; Amphibia: Salamandridae) lend themselves to the study of sequential female mate choice because males are sexually dimorphic (they develop large dorsal crests during the breeding season), females mate with up to seven different males (Halliday and Verrell, 1984; Hosie, 1992) during up to three months, and last male sperm precedence has been suggested (Pecio and Rafinski, unpublished data). Female assessment of males is confined to aspects of male phenotype and courtship vigor (Halliday, 1977) and females do not gain any material resources from their partners, such as paternal care or oviposition sites (Verrell and McCabe, 1988). In addition, large-crested males represent high-quality males because crest height is an honest indicator of phenotypic vigor and recent foraging intake (Green, 1991).

Based on the breeding biology of smooth newts, we tested Halliday's (1983) hypothesis using *T. v. vulgaris*. We predict that there will be no significant difference in the number of females that mate with high- or low-crested males early in the breeding season and that later in the breeding season, significantly more females will mate with males that have higher dorsal crests.

METHODS

Breeding biology

The breeding season of smooth newts extends for up to three months in the spring with mating activity most intense during April and May (Verrell and Halliday, 1985). Receptive females outnumber males in the breeding population at the begin-

Received 16 February 1996; accepted 23 May 1996.

1045-2249/97/\$5.00 © 1997 International Society for Behavioral Ecology

Table 1
Experimental design of sequential mate choice

Treatment	N	Initial pairing				20 days	Second pairing		Final pairing
		Days					Days		
		1	2	3	4		1	2	
1	26	Low	Low	Low	Low	---→ ---→	High	High	If no response
2	28	High	High	High	High		Low	Low	
									Next hour
									High
									High

Females were paired in the initial pairing with high- or low-crested males, then given 20 days to lay eggs, and then remated in the second pairing with a male with an opposite extreme in crest height from the male with which the female first mated. If a female did not remate, she was mated with an extra-high-crested male within the next hour (final pairing) to determine the level of her receptivity. Crest heights were 1 SD beyond the population mean.

ning of the season, but this decreases as the season progresses (Verrell and Halliday, 1985). Females lay eggs throughout the season and, once they begin laying eggs, become less receptive to males. Females become receptive again between bouts of egg laying and within approximately 20 days of their last mating episode (Hosie, 1992; Verrell and Halliday, 1985; Verrell and McCabe, 1988).

Females lay eggs singly and these are individually fertilized as they pass by the spermatheca where sperm are stored (Verrell and Sever, 1988). Pecio and Rafinski (unpublished data) suggested that this process promotes sperm competition with last male paternity in smooth newts, based on their hybridization studies using *T. vulgaris* and a sympatric species, *T. montandoni*. Female smooth newts that are not inseminated during the breeding season deposit unfertilized eggs, suggesting that sperm from the previous year are either not retained or are incapable of fertilization (Pecio, 1992).

Green (1991) and Hosie (1992) showed that females accept a greater proportion of spermatophores deposited by males with greater tail heights than by males with smaller tail heights. Further, Green (1991) found that increased crest height is positively correlated with increased food intake hence large crested males represent high-quality males. However, Halliday (unpublished data) found that males kept on a reduced food supply maintained their crest heights but produced fewer spermatophores than those that received abundant food. Male crest heights increase throughout the reproductive season and reach maximal development from April to June (Griffiths and Mylotte, 1988), but the extent of increase varies greatly among individual males (Verrell et al., 1986). Females appear to differentiate between familiar and unfamiliar males as they prefer to mate with unfamiliar males (Hosie, 1992).

Experimental procedure

Females and males of *T. v. vulgaris* were collected before mating from a drift fence around a pond in Milton Keynes, England (February–March 1994). They were maintained in outdoor tanks (60 × 28 × 37 cm deep) within a larger outdoor tub filled with water to buffer extreme temperature changes. We placed water, gravel, plants, and bricks in each tank, and temperature ranged from 0°C–12°C daily. Newts were fed live zooplankton, *Tubifex*, and cut-up earthworms ad libitum. We maintained males and females separately and placed no more than 30 individuals in each tank. We measured snout-vent length (SVL) to the anterior end of the cloaca in males and females. We measured male crest height in terms of tail height at the deepest section of the tail. Tail height is strongly correlated with crest height (Baker, 1992) and can be considered synonymous with crest height because the crest is continuous along the dorsum to the tail (tail height is usually reported

because it is easier to measure and results in more accurate measurements). We measured male tail heights weekly before testing by laying the deepest section of their tails flat against a ruler.

Experimental design

The design consisted of two treatments (Table 1) using female *T. v. vulgaris* with $N = 26$ for treatment 1 and $N = 28$ for treatment 2. In treatment 1, during the initial pairing a female was paired with one male with a low crest height for four days. She was then given 20 days to lay eggs and then paired in the second pairing with a high-crested male. In treatment 2, a female was paired in the initial pairing with a high-crested male for four days, then given 20 days to lay eggs and then paired in the second pairing with a low-crested male. Male crest heights were at least 1 SD above (high-crested) or below (low-crested) the mean of the males collected.

In the initial pairing, a female was paired once on each of four days with either a low-crested male (5.0–6.5 mm) or a high-crested male (8.5–10 mm) but only one sperm transfer was allowed. As such, the only day that was used for our statistical analysis was the day on which successful sperm transfer occurred. We prevented females from picking up more than one sperm cap by briefly placing a 10 cm net between pairs just before males put down more spermatophores. This allowed a female to be stimulated by being successively courted by a male while still controlling the number of sperm transfers each female received. Females that are not sufficiently stimulated by courtship in the initial pairing often do not lay eggs (Halliday, personal observation), therefore we paired females with the same male for four days. Logistics made it such that females had to be paired with the same male so that there was no unknown change in female perception caused by variation between males.

Females were remated in the second pairing if sperm transfer occurred in the initial pairing. In the second pairing, a female was paired with a high- (9.0–11.0 mm in treatment 1) or a low- (4.0–6.5 mm in treatment 2) crested male. Male crest heights were different (by at least 3 mm) from the crest heights of the previous males with which females had been paired (Table 1). First we determined whether males were in courtship condition by using a harnessed female to simulate a responsive female (for method, see Halliday, 1975). If males began to court the harnessed female, they were used in the second pairing. Thus, all males used in the second pairing and in the final pairing stages were receptive to females.

In the second pairing, a female was paired with the same male for 1 h during one evening and 1 h the next morning. If sperm transfer did not occur in the second pairing on either day, a female was paired in the final pairing (within 1 h of her last pairing on the second day) with a male that had

Table 2
Results of sequential mate choice experiment

Initial pairing			Second pairing			Final pairing		
Male	No. females		Male	No. females		Male	No. females	
Crest	Mating	Not mating	Crest	Mating	Not mating	Crest	Mating	Not mating
Low	14	12	High	11	3	Extra-high	3	0
High	16	12	Low	0	16	Extra-high	10	6
$\chi^2 = 0.059$, $df = 1$, $p = .81$			$\chi^2 = 19.85$, $df = 1$, $p = .0001$					

an extra-high crest (10–13 mm, which was at least 2 mm higher than the previous male that she had encountered) to determine the level of her receptivity. Encounters were considered unsuccessful if either a male displayed to a female but she never approached him or he put down one or more spermatophores but no sperm transfer occurred.

Protocol

On the morning before each testing day, the test males and females were taken to the laboratory and placed in storage tanks (34 × 38 × 26 cm deep) with gravel, plants, and food for the four testing days. Testing temperatures ranged from 16°C–19°C. Testing was performed from 13 March through 23 April 1994 during the middle of the breeding season.

When testing began, the test females were placed in separate test chambers (29 × 28 × 37 cm deep) for 1 h to habituate and then the test males were placed in the chambers for 15 min before testing. Males and females were separated by a Plexiglas divider during habituation. Test chambers had gravel on the bottom and were filled with aged tap water. After the habituation period, the divider was carefully removed, allowing the male and female to interact. Males were given up to 1 h (average courtship time: Halliday, 1974) to start courtship before an encounter was considered unsuccessful.

During these interactions, we recorded (1) time to sperm transfer from the time the pair first oriented to each other (i.e., a successful courtship) and (2) the number of times that males deposited spermatophores. Latency to sperm transfer and the number of spermatophores deposited before sperm transfer occurs can be used to assess female receptivity.

Males were returned to their outdoor tanks after each pairing session. Females from successful courtships (i.e., sperm transfer occurred) were placed in separate egg-laying chambers (27 × 16 × 11.5 cm deep) with gravel, live plants, and zooplankton (12°C–16°C). The chambers were placed in front of a large open window with a natural photoperiod. Eggs laid by females were counted and collected daily and were maintained in separate chambers to determine whether the eggs were fertilized.

All encounters within each treatment were randomized based on the assigned number of each male and female. Comparisons between the initial pairing and the second pairing were analyzed using a 2 × 2 contingency test (Siegel and Castellan, 1988). We used a two-tailed Wilcoxon signed-rank test to compare latency to sperm transfer within a treatment and a two-tailed Wilcoxon-Mann-Whitney test to compare between the two treatments (Siegel and Castellan, 1988). Spearman rank correlation tests were used for correlational analyses. All analyses used $\alpha = 0.05$.

RESULTS

There was no significant difference in the frequency of mating or not mating in the initial pairing between the two treat-

ments (Table 2). In the second pairing (Table 2), significantly more females mated with high-crested males than with low-crested males. Note that not a single female that had previously mated with a high-crested male was subsequently willing to mate with a low-crested male. In the final pairing, females that had not mated with the previous male frequently mated with the extra-high-crested male in both treatments (Table 2).

There was no significant difference in mean latency to sperm transfer in treatment 1 between initial pairing (low-crested males) and second pairing (high-crested males) (Figure 1A). Mean time was measured from the time a male first oriented toward a female in a successful courtship. In treatment 2, sperm transfer was significantly faster in the final pairing (extra-high-crested males) than in the initial pairing (high-crested males) (Figure 1B). There was no significant difference in mean time to sperm transfer during initial pairings between treatment 1 and 2 [two-tailed, Wilcoxon-Mann-Whitney test, $N = 30$, $z = -.287$, $p = .77$] (cf. left bars in Figure 1A and 1B). Significantly more females ($N = 5$) picked up sperm caps deposited earlier by males than sperm caps deposited later in the courtship sequence during the initial pairing (Spearman rank correlation test, $r_s = -1$; $p < .05$).

There was no significant difference in the frequency of laying eggs or not between the two treatments ($\chi^2 = 0.621$; $df = 1$; $p = .4308$); nine of 14 females laid eggs when paired with a low-crested male and eight of 16 laid eggs when paired with a high-crested male in the initial pairing. There was no significant correlation between male tail height in the initial pairing with the number of eggs laid by females during the 20 days ($N = 19$; $r_s = -.071$; $p > .5$). Similarly, there was no significant correlation between the latency to remate in the second pairing and the number of eggs laid ($N = 16$; $r_s = .15$; $p > .5$). There was no significant correlation between male SVL and tail height in the initial pairing ($N = 23$; $r_s = -.075$; $p > .5$) or between SVL and tail height in the second pairing ($N = 31$; $r_s = -.205$; $p > .20$). Power analysis was not used on non-significant results because strong inferences were not drawn.

DISCUSSION

Our experiment has shown a clear difference in female choosiness between the first and second pairings. Upon encountering the first male of the courtship season, females showed no obvious preference for mating with low-crested males (accepted by 14 of 26 females) or high-crested males (accepted by 16 of 28 females). Subsequently, female smooth newts showed mate choice by remating only with males that had high dorsal crests. These results suggest that females initially will mate with any male, but subsequently they will remate only with males that have larger crests and hence represent higher-quality mates as suggested by Green (1991). These data, then, support our prediction from Halliday's hypothesis (1983).

While last male sperm precedence occurs in many species

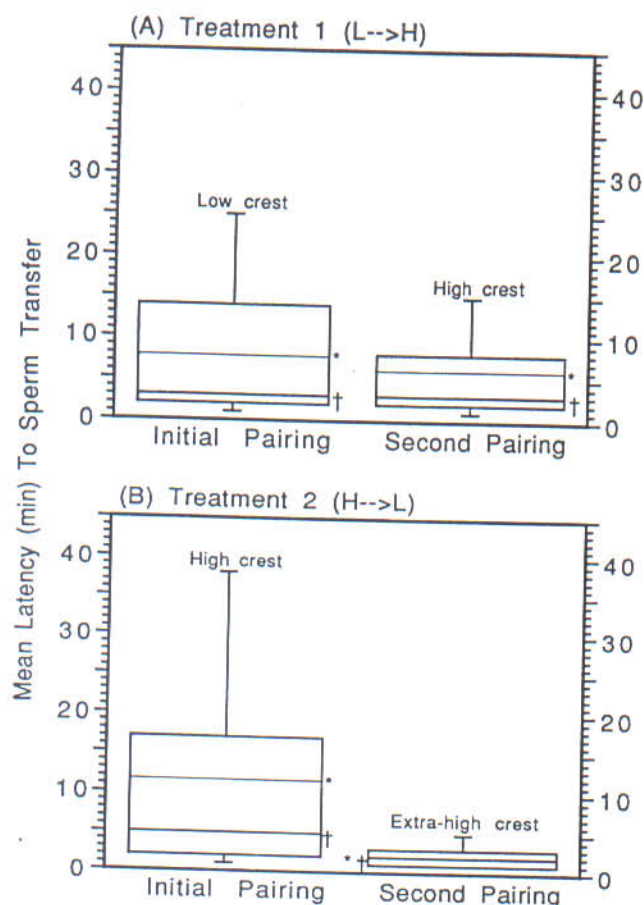


Figure 1
Comparison of latency (in minutes) to sperm transfer (A) in treatment 1 between the initial pairing and the second pairing (Wilcoxon test, $N = 9$, $T^* = 22.5$, two-tailed $p > .9$) and (B) in treatment 2 between the initial pairing and the final pairing ($N = 10$, $T^* = 47.5$, two-tailed $p = .04$). Mean time was measured from the time that a male first oriented toward a female. The upper and lower horizontal lines of the box plot represent the first and third quartiles, the median is represented by \dagger , and the mean is represented by $*$.

(Thornhill and Alcock, 1983) and has been suggested for smooth newts (Pecio A and Rafinski J, unpublished data), it is not essential for supporting Halliday's hypothesis (1983). Even if sperm of several males are mixed within a female's spermatheca, a female would still gain by mating with higher-quality males as some of her progeny would be fathered by these males.

An alternative hypothesis is that female smooth newts may be less choosy about male quality earlier in the season for some reason; e.g., there may be a female-biased sex ratio in their natural environments. Later in the season, as fewer females are mating and more males are available, females may become more choosy and mate only with high-crested males. This alternative hypothesis about female mate decision rules does not require that females compare a prospective mate with a previous mate. Our experimental design does not allow us to rule out this competing hypothesis.

Crowley et al. (1991) predicted that low- and high-quality females will choose high-quality males until the end of the breeding season when size assortative mating will occur. This model is based on females that mate multiply during a short life span (up to 1 year) whereas smooth newts mate multiply within each of numerous breeding seasons. The results of our

experimental condition are inconsistent with this prediction. Moreover, we examined female choice in the middle of the courtship season, so the predictions for the end of the season were not tested by our experiment.

Females did not show any significant difference in the latency to sperm transfer between small- and large-crested males in the initial pairing. Also there was no significant difference in the latency to sperm transfer between treatment 1 in the initial pairing and in the second pairing, hence the null hypothesis that there was no difference in the courtship activity of smaller- and larger-crested males could not be rejected (Figure 1A). Male choice of mates may have influenced the outcome of these two pairings, but this cannot be determined from our data.

The null hypothesis that there was no difference in the amount of sperm in a single sperm cap from a large- or a small-crested male could not be rejected based on the non-significant correlation between male crest height in the initial pairing and the number of eggs laid by females in 20 days. The number of eggs laid also did not significantly affect the latency to sperm transfer when females were remated. Therefore, the need for sperm replenishment does not appear initially to affect the willingness of females to remate. Moreover, if females remate purely to insure that they have sufficient sperm, then they would also remate with small males, which did not occur.

In the second pairings of our experiment, 11 of 14 females remated with higher-crested males while zero of 16 remated with lower-crested males, suggesting that females are choosing males based only on their crest height and not on body size. There was no significant correlations (in the initial pairing and the second pairing) between crest height and SVL. This lack of correlation also suggests that the development of male crests may be a result of sexual selection through female preference for males with larger crests but this needs to be explored further.

In the second pairing, we used only males that we had determined were motivated to mate. Yet, in treatment 2 during the second pairing, sperm transfer did not occur when females were paired with small-crested males. Instead, sperm transfer occurred only when females were paired with the extra-high-crested males in the final pairing. In fact, the latency to sperm transfer in the final pairing was significantly faster than in the initial pairing. These females were, therefore, more receptive to a higher-crested male than their previous mate. Interestingly, many (10 of 16) of the females in treatment 2, during the final pairing, approached the larger-crested males as soon as they were placed into the tank, hence the short mean time to sperm transfer (Figure 1B). These females may have been more willing to remate with an extra-high-crested male because there was a large phenotypic difference between him and the previous male that the females had seen in the second pairing (low crest). This suggests that previous experience with other males may have influenced subsequent female choice. Three other studies have also suggested that previous experience of a female (i.e., previous male effect) influences female choice of association (Bakker and Milinski, 1991; Collins, 1995) and female choice of a mating (Downhower and Lank, 1994), but these studies did not involve females that mate multiply.

It is unlikely that female smooth newts use threshold decision rules (for a review, see Real, 1990) to choose males, because male crest height increases during the breeding season and may vary between seasons (Griffiths and Mylotte, 1988). If females used a threshold rule to choose males and this standard consisted of a larger crest height than that found in the population early in the breeding season, then no females would mate until late in the breeding season. Under these

conditions, females would spend an important part of the season sampling males without mating and thus would start the lengthy egg-laying process (requiring three months: Verrell and Halliday, 1985) considerably later than they otherwise could. Therefore, fixed-threshold decision rules are unlikely to provide an adaptive strategy for female smooth newts. A relative choice process (Real, 1990), on the other hand, combined with multiple mating, would allow female smooth newts both to initiate egg-laying very early in the season and, subsequently, to mate preferentially with higher-quality males. In conclusion, female smooth newts become more selective of mates as the season progresses. This suggests that female mate choice behavior might function to increase the quality of their offspring. Therefore smooth newts conform to Halliday's (1983) prediction for species in which females mate multiply with different males, store sperm, and gain no other resources from males.

We are grateful to P. Verrell for help with the experimental design; R. Jaeger for helpful discussions and unfaltering aid in the writing of this manuscript; J. Baker for collecting newts; C. Boake, M. Dyson, R. Harris, R. Jaeger, P. Verrell, and an anonymous reviewer for comments on the manuscript; C. Hosie and V. Waights for logistical support; and B. Quinn for additional support. This research was supported in part by funds from the Graduate Student Organization at The University of Southwestern Louisiana, a grant from the Society of Sigma Xi to C.G., National Science Foundation grant DEB-9314081 to R.G. Jaeger and by Louisiana Board of Regents Doctoral Fellowship LEQSF (1993-98)-GF-20 to C.G. through R.G. Jaeger.

REFERENCES

- Andersson M, 1986. Sexual selection and the importance of viability differences. *J Theor Biol* 120:251-254.
- Arak A, 1988. Female mate selection in the natterjack toad: active choice or passive attraction? *Behav Ecol Sociobiol* 22:317-327.
- Baker JM, 1992. Body condition and tail height in great crested newts, *Triturus cristatus*. *Anim Behav* 43:157-159.
- Bakker TCM, Milinski M, 1991. Sequential female choice and the previous male effect in sticklebacks. *Behav Ecol Sociobiol* 29:205-210.
- Brown L, 1981. Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Anim Behav* 29:375-382.
- Collins SA, 1995. The effect of recent experience on female choice in zebra finches. *Anim Behav* 49:479-486.
- Crowley PH, Travers SE, Linton MC, Cohn SL, Sih A, Sargent RC, 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *Am Nat* 137:567-596.
- Dale S, Amundsen T, Lifjeld JT, Slagsvold T, 1990. Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behav Ecol Sociobiol* 27:87-91.
- Dale S, Rinden H, Slagsvold T, 1992. Competition for mate restricts mate search of female pied flycatchers. *Behav Ecol Sociobiol* 30:165-176.
- Davies NB, 1992. *Dunnock behaviour and social evolution*. Oxford: Oxford University Press.
- Downhower JF, Lank DB, 1994. Effect of previous experience on mate choice by female mottled sculpins. *Anim Behav* 47:369-372.
- Green AJ, 1991. Large male crests, an honest indicator of condition, are preferred by female smooth newts, *Triturus vulgaris* (Salamandridae) at the spermatophore transfer stage. *Anim Behav* 41:367-369.
- Griffiths RA, Mylotte VJ, 1988. Observations on the development of the secondary sexual characters of male newts, *Triturus vulgaris* and *T. helveticus*. *J Herpetol* 22:476-480.
- Halliday TR, 1974. Sexual behavior of the smooth newt, *Triturus vulgaris* (Urodela: Salamandridae). *J Herpetol* 8:277-292.
- Halliday TR, 1975. An observational and experimental study of sexual behaviour in the smooth newt, *Triturus vulgaris* (Amphibia: Salamandridae). *Anim Behav* 23:291-322.
- Halliday TR, 1977. The courtship of European newts: An evolutionary perspective. In: *Reproductive biology of amphibians*, (Taylor DH, Guttman SI, eds). New York: Plenum; 185-232.
- Halliday TR, 1983. The study of mate choice. In: *Mate choice*, (Bateson P, ed). Cambridge: Cambridge University Press; 3-32.
- Halliday TR, Arnold SJ, 1987. Multiple mating by females: a perspective from quantitative genetics. *Anim Behav* 35:939-941.
- Halliday TR, Verrell PA, 1984. Sperm competition in amphibians. In: *Sperm competition and the evolution of animal mating systems*, (Smith RL, ed). New York: Academic Press; 487-508.
- Hosie C, 1992. Sexual motivation and mate choice in the female smooth newt, *Triturus vulgaris* (PhD dissertation). Milton Keynes: The Open University.
- Janetos AC, 1980. Strategies of female choice: a theoretical analysis. *Behav Ecol Sociobiol* 7:107-112.
- Janetos AC, Cole BJ, 1981. Imperfectly optimal animals. *Behav Ecol Sociobiol* 9:203-209.
- Knapp RA, Kovach JT, 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behav Ecol* 2:295-300.
- Pecio A, 1992. Insemination and egg laying dynamics in the smooth newt, *Triturus vulgaris* in the laboratory. *J Herpetol* 2:5-7.
- Real L, 1990. Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 136:376-404.
- Ryan MJ, 1985. *The Tungara frog: A study in sexual selection and communication*. Chicago: University of Chicago Press.
- Siegel S, Castellan NJ Jr., 1988. *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill Book Company.
- Sims ME, Ball GF, Cheng M, 1989. Sperm competition after sequential mating in the ringed turtle-dove. *Condor* 89:112-116.
- Small MF, 1992. Female choice in mating. *Am Sci* 80:142-151.
- Thornhill R, Alcock J, 1983. *The evolution of insect mating systems*. Cambridge, Massachusetts: Harvard University Press.
- Verrell PA, Halliday T, 1985. Reproductive dynamics of a population of smooth newts, *Triturus vulgaris* in southern England. *Herpetologica* 41:386-395.
- Verrell PA, Halliday TR, Griffiths ML, 1986. The annual reproductive cycle of the smooth newt (*Triturus vulgaris*) in England. *J Zool, Lond (A)* 210:101-119.
- Verrell P, McCabe N, 1988. Field observations of the sexual behaviour of the smooth newt, *Triturus vulgaris vulgaris* (Amphibia: Salamandridae). *J Zool, Lond (A)* 214:533-545.
- Verrell PA, Sever DM, 1988. The cloaca and spermatheca of the female smooth newt, *Triturus vulgaris* (Amphibia: Urodela: Salamandridae). *Acta Zool (Stockh)* 69:65-70.
- Walker WF, 1980. Sperm utilisation strategies in nonsocial insects. *Am Nat* 115:780-799.
- Wittenberger JF, 1983. Tactics of mate choice. In: *Mate choice*, (Bateson P, ed). Cambridge: University of Cambridge Press; 435-447.