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**Competition and Energetic Constraints  
in the Courting Great Crested Newt, *Triturus cristatus*  
(Amphibia: Salamandridae)**

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**Abstract**

The sexual behaviour of *Triturus cristatus cristatus* consists of a prolonged period of static display, with bouts containing the two different tail movements Lash and Fan, followed by spermatophore transfer. There is evidence that Fanning fatigues males and that its rate and duration are under energetic constraints. The frequency of Fanning (Hz) drops gradually during a bout, and bouts get shorter as time goes on while the intervals between bouts get longer. Males who use more bouts have longer intervals between them. As a male undergoes repeated sessions of static display, the maximum lengths of Fan bouts conducted in each session decrease over time. Hence there are trade-offs between the rate and duration of display activities. These results are consistent with a role of viability-indicator models of intersexual selection in the evolution of the courtship display. When males are courting in the presence of a rival male, they significantly increase the number of Fan beats in each bout and the number of bouts conducted before attempting a mating. They also decrease the duration of intervals between bouts. A solitary male is probably selected to give a shorter, less intense display to a female in order to save time and to prevent the fatigue that would reduce his capacity to display to the next female.

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**Introduction**

European newts, *Triturus*, breed in water during the spring and early summer and live on land the rest of the year. All species of *Triturus* possess complex mating behaviour that involves prolonged display by the male followed by a sequence of stereotyped behaviour patterns required to transfer a spermatophore between partners in the absence of direct pairing through copulation or amplexus (SMITH 1951; HALLIDAY 1977a). Aquatic newts breathe air at the surface, but breathing and courtship are incompatible activities, as courtship

occurs at the bottom of ponds and is terminated whenever one of the partners ascends to breathe. Since males are courting on a limited supply of oxygen, newts are especially likely to be under energetic constraints during courtship.

The courtship of the great crested newt, *Triturus cristatus* (L), has recently been described in detail (GREEN 1989). In the present study, I conduct a detailed analysis of quantitative variation in courtship display, considering both changes in the display produced by one individual over time, and differences between individual males. These analyses serve three main purposes.

Firstly, I look for evidence that the courtship display takes the male to energetic limits. For males of many species, courtship displays are known to be energetically expensive, but there is very little evidence that animals reach energetic limits during a single instance of sexual behaviour (HALLIDAY 1987). It is particularly important to look for such constraints because, by revealing which males have the highest physiological limits, they potentially allow females to choose mates with higher general fitness. For example, the ability of males to expend energy at a high rate during courtship may be correlated with a similar ability for a high rate of exertion during predator avoidance or foraging. Assuming heritability, energetic limits are thus consistent with viability-indicator models of intersexual selection (BRADBURY & ANDERSSON 1987).

Secondly, I consider how males respond to the presence of competing males. Because of the imbalance in gamete investment, male animals are generally expected to attempt mating whenever possible (PARTRIDGE & HALLIDAY 1984). Hence they are often predicted to produce as attractive a display as possible when courting a female. However, if there are significant costs to display, males might be expected to pay a higher cost in the presence of other males, as intrasexual competition reduces the chances of achieving a mating with a low cost display. If a courtship display takes a male to energetic limits and causes fatigue, then there are costs to intensifying the display given to a female, in that it reduces a male's capacity to display to a second female.

Thirdly, I attempt to explain observed variation in courtship behaviour on the basis of male size and tail height, and female size. Relating variation in sexual displays to body size and the size of morphological characters of males sheds light on the sexual selection forces acting on these male features. For example, if larger males display at a higher intensity or longer duration, this is likely to give them a selective advantage. Males might be expected to display more vigorously to larger females, as they are likely to have a higher fecundity and so may offer a higher resource value to the male (VERRELL 1986; VERRELL et al. 1986).

Finally, I also relate variation in male display to population differences. This results from the fact that animals had to be collected from different populations, rather than being a main aim of the study.

## Materials and Methods

For full details see GREEN (1989). Observations were conducted during April—May 1986 and March—April 1987. Newts were collected from four ponds in Oxfordshire and the sexes were housed separately in aquaria at 10—12 °C. All observations were conducted in aquaria of 45 × 30 × 30 cm.



The water depth was 12 cm and the temperature was 10–15 °C. The tank was lit by an overhead 25-W incandescent bulb, shone through a correction filter to transform the wavelength distribution to that of daylight. One or two members of each sex were introduced into opposite ends of the tank, separated by a temporary barrier, and left overnight to settle. Males were always placed with females from their own population. The following morning, the barrier was removed and sexual behaviour was recorded for up to 6 h on video. Combined with slow motion playback facilities, this allowed a thorough analysis of newt behaviour.

Immediately after observation, I measured the snout-vent length and maximum tail height of the animals. In 1987, I also measured their tail length. Due to changes in available study populations and laboratory workspace, newts were both collected from different populations and studied at different temperatures in the two years. Because differences in populations and temperature were confounded, by controlling for population differences in multiple regression analyses of courtship variables, I simultaneously controlled for temperature differences. In 1986 only one population was used, and 13 successful observations were made at 15 °C, with one male and one female in each, using 9 different males and 5 different females. In 1987 three populations were used and 21 successful observations were made at 10 °C (16 involved two males and 17 involved two females) using 32 different males and 32 different females.

Data were analyzed with GLIM (Generalized Linear Interactive Modelling system, PAYNE 1986) and Statview (Brain Power Inc. 1986) statistical packages.

## Results

### Outline of Courtship Display

The main display phase of *T. cristatus* is static display (GREEN 1989), in which the female remains static while the male courts from in front. Each discrete period of static display is a 'session' of courtship, consisting of  $13.82 \pm 9.95$  bouts ( $\bar{x} \pm SD$ ) of male tail movements with intervals of  $10.5 \pm 6.7$  s ( $\bar{x} \pm SD$ ) between bouts, when the tail is still (inter-bout interval). There are two basic male displays. The most important is Fan, a regular beating of the tail from side to side at 0.5–0.8 Hz, establishing a current that carries pheromones to the female. Each bout contains  $6.7 \pm 8.2$  Fan beats ( $\bar{x} \pm SD$ ). The number of Fan beats in a bout peaks in the first six bouts of a session, and often the peak bout is much longer than all the others. 15 % of bouts contain the second display, Lash, in which the male hits the female's flank with his tail. This display is more common towards the end of a session, and is often used to stop the female when she begins to walk away from the male. A session is ended when the male begins Creep, a spermatophore transfer behaviour (GREEN 1989). There are usually several sessions in each encounter. The timing of entry into Creep is apparently under the male's control, and the female gives little feedback to the male during static display.

### Fan Beat Frequency

For 31 males, the frequency of Fan beating (Hz) was calculated from a courtship bout with at least 9 Fan beats. Only the most regular beats in the middle of the bout were used to calculate the frequency. Frequency was made the dependent variable (logged to remove heterogeneity of variance) in a multiple regression with the population from which the male was drawn and the presence or absence of a rival male in the tank as fitted factors and snout-vent length, tail height and the number of Fan beats in the measured bout as fitted continuous

Table 1: Multiple regression of Fanning frequency (Hz) of male *T. cristatus* (predictor variables)

Snout-vent length	Tail height	No. of Fan beats/bout	Pres. or abs. of a rival male	Male popul.	$r^2$	F	df
+0.24	-0.33	-2.69*	0.00	0.66	0.638	5.79***	7,23

t values are given for the partial effects of male snout-vent length, tail height and number of Fan beats in the bout. + and - denote the sign of the regression slope. F values are given for the partial effects of presence or absence of a rival male and male population.  $r^2$ , F, and df refer to the whole regression. \*  $p < 0.05$ , \*\*\*  $p < 0.001$

variables (Table 1). The partial effect of number of beats was significant ( $p = 0.013$ ); in longer bouts Fanning has a lower frequency (Fig. 1). No other variable had a significant partial effect. There was no significant interaction between the presence or absence of a rival and the effect of bout length on frequency ( $F_{1,22} = 0.78$ , ns). When the date of the observation or the snout-vent length of the female courted were added to the regression, they had no significant effect on Fanning frequency and did not change the effect of the number of beats in the bout. The length or height of the tail might be expected to influence the resistance offered by the water to a moving tail, and so influence the frequency of Fanning. However, neither snout-vent length (highly correlated with tail length,  $r = 0.55$ , GREEN in prep.) nor tail height were significant predictors of Fan frequency (Table 1). In a second regression on a subset of males for which tail length was measured ( $n = 23$ ), there was no evidence for any effect of tail length on Fan frequency.

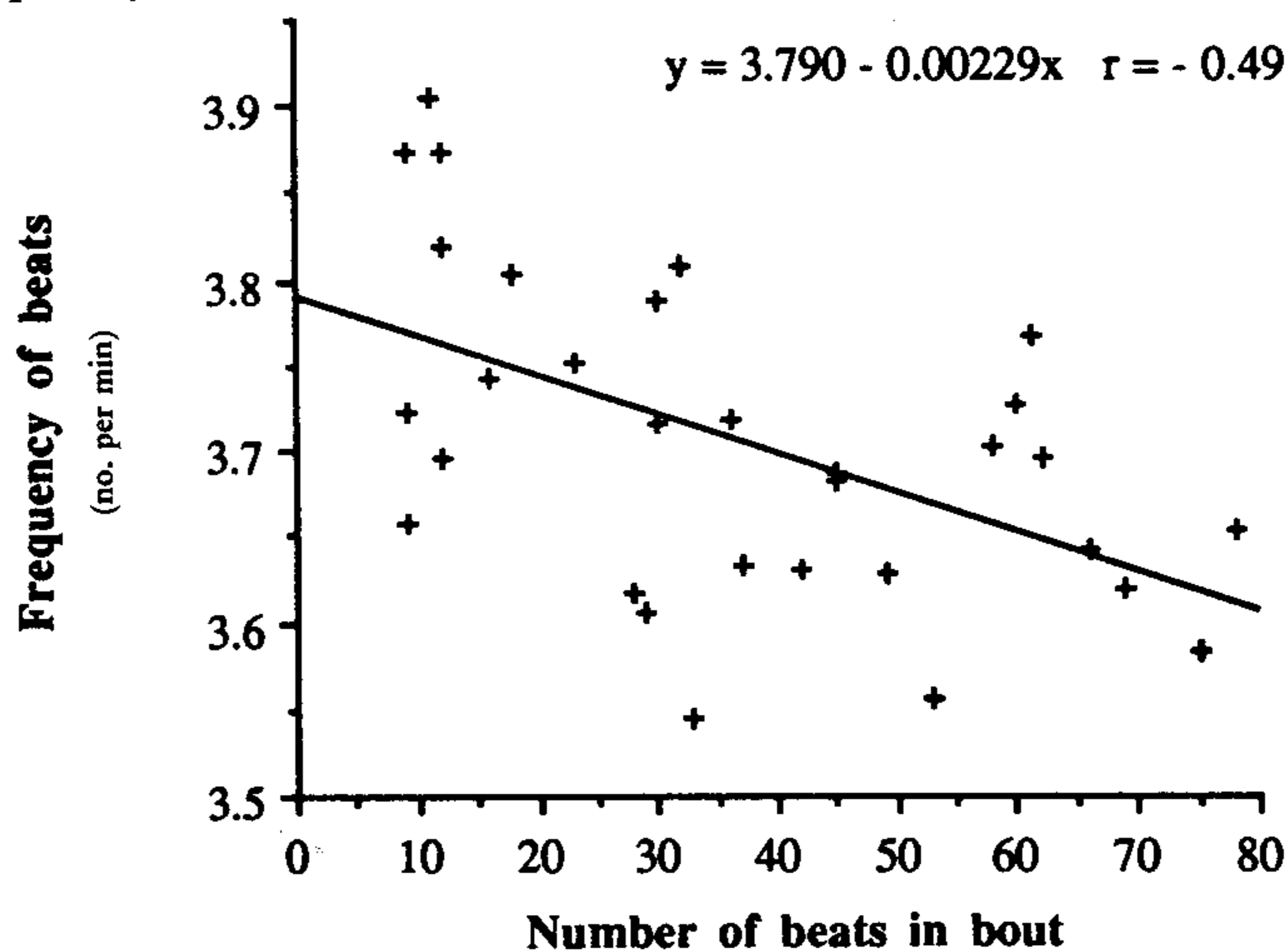


Fig. 1: Scattergram of frequency of Fan beats for 31 male *T. cristatus* versus number of beats in the bout. The frequencies plotted are corrected for the effects of male snout-vent length, tail height, presence or absence of a rival and population by subtracting the fitted multiple regression estimates for their effects from the actual frequencies observed. There is a significant correlation between number of beats and frequency ( $p = 0.013$ ). Values of  $p$  and  $r$  are calculated from the original regression



The reason for the negative correlation between the number of Fan beats in a bout and the frequency of Fanning is that Fan beats gradually become slower as a bout progresses. For six males I measured the duration of every Fan beat in a single long bout, and then conducted a separate regression for each male with beat duration as the dependent variable and the chronological order of the beats as the predictor. For each male, beat duration increased significantly as the bout progressed (Table 2).

Table 2: Regressions of the duration of single Fan beats from one bout on the chronological order of the beat within the bout for six male *T. cristatus*

Male	Date	n	$\bar{x}$	SD	r
1	17. 4. 86	67	1.29	0.06	0.433***
2	21. 4. 87	34	1.81	0.11	0.515**
3	23. 4. 87	74	1.77	0.17	0.504***
4	23. 4. 87	28	1.96	0.21	0.511**
5	24. 4. 87	64	1.88	0.16	0.252*
6	24. 4. 87	52	1.63	0.15	0.331*

Separate regressions were conducted for one bout for each male. For males 1 to 5, this was the longest single bout performed by the male. Male 1 courted alone while the other males had a rival male present in the courtship tank. n: number of consecutive Fan beats measured in the bout,  $\bar{x}$  and SD are of beat duration (s). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

For each of 24 males, Fan beat frequency was calculated twice from two different bouts, separated in time by 5—240 min (median = 58 min). As expected, the bout with the most beats had the lower frequency (two tailed one sample t test,  $t = 3.39$ , 22 df,  $p < 0.005$ ). As well as changing within bouts, the Fanning frequency may change over time between bouts. With the coefficient from the above regression for the effect of number of beats in a bout on frequency, I corrected the change in frequency between the first and the second measure for each male for the difference in the number of beats. The corrected changes did not differ significantly from zero ( $t = 1.28$ , 23 df, ns).

#### Variation in Static Display within Males

The first observed completed sessions of static display (i.e. those ending in Creep, GREEN 1989) of five or more bouts from 20 males were used to analyze the changes in the length of interbout intervals with sessions. First, any interval was excluded when it or the preceding bout contained any of the following events considered likely to change the normal duration of the interbout interval: a movement of either sex, a Lash or a bout misdirected to the posterior instead of the anterior end of the female. For each male, I then conducted a Spearman rank correlation between the inter-bout interval and its chronological order within the session. The 20 correlation coefficients were then collectively subjected to a two tailed Wilcoxon test, in order to test for an overall deviation from zero. The coefficients were found to be significantly greater than zero (median  $r_s = 0.545$ ,

$T = 19$ ,  $p < 0.002$ ). This method of analysis is appropriate because it reduces data for one male to one number, and so takes into account the fact that multiple observations from each male are not independent. This process was repeated for the time length of bouts, and the coefficients of correlation between bout length and order were significantly negative (median  $r_s = -0.527$ ,  $T = 33$ ,  $p < 0.008$ ). Hence, as a session proceeds, the bouts get shorter and the intervals between bouts get longer.

These analyses pool data from 7 males who were courting alone and 13 males courting with a second male in the tank. When these two sets of males were analyzed separately, the two effects of bout duration decreasing and interval duration increasing during sessions remained significant for males with a rival ( $p < 0.005$ ), but were not significant for single males, although the direction of the effect remained. The correlation coefficients between inter-bout interval and order were more positive in the presence of a rival male, but not significantly so (two tailed Mann-Whitney U test,  $U = 28$ , ns). Similarly the coefficients between bout duration and order were more negative in the presence of a rival, but not significantly so ( $U = 30$ , ns).

In an analysis of changes in the peak bout length in sessions over time, the longest of the first six bouts (length in number of Fan beats) was counted for each session of six or more bouts, whether it was a completed session (i.e. ending in a Creep) or not. Spearman rank correlations were then conducted between chronological session order and peak bout length for each of 30 males. Then the 30 correlation coefficients were analyzed with a one tailed Wilcoxon one sample signed-rank test for a significant deviation from zero. There was a significant decrease in peak bout length over time (median  $r_s = -0.23$ ,  $n_{\text{for test}} = 29$  males,  $T = 136.5$ ,  $p = 0.04$ ). Sessions were separated by intervals of  $10.4 \pm 18.2$  min ( $\bar{x} \pm \text{SD}$ ,  $n = 375$ , range 0.9—212 min, median = 4.9 min).

This analysis pools data from 10 males that were courting alone and 20 males courting in the presence of a rival male. When the two sets of males were analyzed separately, the effect remained significant for males with a rival ( $p < 0.05$ ) but is not significant for single males, although the direction of the effect remained. The correlation coefficients between peak bout duration and order are more negative in the presence of a rival but not significantly so (one tailed Mann-Whitney U test,  $U = 99.5$ , ns).

In the above analyses, for males who deposited a spermatophore, only those sessions observed up to the first deposition were considered, in order to control for any effects resulting from deposition rather than from time spent in courtship. However, of six males who deposited, there were no obvious differences between sessions before and after a deposition in the number and length of bouts, inter-bout intervals or the number of lashes (two tailed Wilcoxon tests, ns).

#### Variation in Static Display between Males

There is considerable variation in the number of courtship bouts, the duration of bouts and the duration of inter-bout intervals conducted by different males during static display. For 31 males, I attempted to explain this variation on



the basis of differences in the populations from which males were drawn, whether or not the male was courting in the presence of a rival male, and the snout-vent length and tail height of the males. I analyzed four parameters of static display in turn for effects of these variables, using multiple regression analyses that included male population and the presence or absence of rivals as fitted factors, and snout-vent length and tail height as fitted continuous variables (Table 3).

Table 3: Multiple regression of variables of courtship sessions conducted by male *T. cristatus*

Snout-vent length	Tail height	No. of bouts/session	Pres. or abs. of a rival male	Male popul.	r <sup>2</sup>	F	df
1. +0.77	-1.05		0.32	0.89	0.161	0.61	6,19
2. +1.37	+0.79		10.75**	2.88	0.677	4.89**	6,14
3. +2.56*	-1.14	-0.89	13.74**	3.16	0.926	23.40***	7,13
4. -0.70	-0.85	+2.89*	12.96**	3.87*	0.665	3.69*	7,13

Dependent variables: 1. Maximum length of any one Fan bout(s), 2. maximum number of Fan bouts in a completed session, 3. median length of Fan bout(s) in the longest completed session, 4. median length of inter-bout interval(s) in the longest completed session. Predictor variables: top line. t values are given for the partial effects of male snout-vent length, tail height and number of bouts in the session. + and - denote the sign of the regression slope. F values are given for the partial effects of rival males and male populations. Blanks indicate the predictor was not included in the model. r<sup>2</sup>, F and df refer to the whole regression. \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.0001

#### *Maximum Fan bout duration*

Fan bouts fall into two classes (GREEN 1989). The majority are normally distributed with up to 13 beats and a mode of 6. There are also occasional bouts with many more beats (maximum = 163). The maximum duration (s) of any one Fan bout by each male was made the dependent variable in a multiple regression (logged to remove heterogeneity of variance). This was an attempt to find predictors of the lengths of those extraordinarily long bouts, so I only included males with bouts of more than 13 beats in this regression ( $\bar{x} \pm SD = 53.96 \pm 32.62$  beats, n = 26). None of the predictor variables had a significant effect in this regression (Table 3). When the date of observation or the snout-vent length of the female courted during the bout were added to the regression, neither had a significant partial effect. Similar results were obtained for this regression when the maximum number of Fan beats in a bout was used as the dependent variable instead of the maximum number of s, or when males who never conducted bouts with more than 13 beats were included.

#### *Maximum session length*

The maximum number of bouts in a completed session for each male was made the dependent variable in a multiple regression (logged to remove heterogeneity of variance). There was a highly significant partial effect of the

presence of a rival ( $p < 0.006$ , Table 3). Males conducted more bouts in a courtship session when another male was present in the tank. When the date of the observation or female snout-vent length were added to the regression, they did not have significant effects and did not remove the effect of the presence of a rival.

#### *Median bout duration*

The duration (s) of the median bout in the longest completed session for each male was made the dependent variable in a multiple regression, with the number of bouts in the session as one of the predictors. There was a significant positive partial effect of snout-vent length ( $p < 0.025$ ) and a highly significant partial effect of the presence of a rival ( $p < 0.003$ , Table 3). Males conducted longer Fan bouts in a courtship session when another male was present, and larger males used longer bouts. There was no significant interaction between the presence or absence of a rival and the effect of snout-vent length on bout length ( $F_{1,12} = 1.73$ , ns). When the date of the observation or female snout-vent length were added to the regression, they did not have significant effects and did not remove the effect of the presence of a rival. However, a weak interaction was found between date and male population (i.e. the slope of the effect of date on bout duration differs between populations,  $F_{2,10} = 4.28$ ,  $p < 0.05$ ), and when this was included, the partial effect of snout-vent length was no longer significant. Therefore, there are not strong grounds for concluding that snout-vent length has a direct effect on Fan bout duration. Similar results were obtained when the median number of Fan beats in a bout was used as the dependent variable instead of the median number of s.

#### *Median inter-bout interval*

The duration (s) of the median inter-bout interval in the longest completed session for each male was made the dependent variable in a multiple regression, with the number of bouts in the session as one of the predictors. There was a significant partial effect of the number of bouts in a session ( $p < 0.013$ ), a significant partial effect of population ( $p < 0.04$ ) and a highly significant partial effect of the presence of a rival ( $p < 0.004$ , Table 3). Males used shorter inter-bout intervals in the presence of a rival and longer intervals in longer sessions. There was no significant interaction between the presence or absence of a rival and the effect of session length on inter-bout interval ( $F_{1,12} = 0.63$ , ns). The population effect is ambiguous as males of one population (that used in 1986) courted at a higher temperature than those of the other three. The effect may be the results of males using shorter inter-bout intervals in warmer water, because there was no significant difference between the three populations studied at the same temperature in 1987 ( $F_{2,13} = 0.91$ , ns).

When the date of the observation or female snout-vent length were added to the regression, they did not have significant effects and did not remove the effects of the presence of a rival, the number of bouts in the session, or the population.



## Discussion

### Effects of Intrasexual Competition

Courting male *T. cristatus* respond to the presence of another male by increasing the duration and intensity of their static display to females in three ways. They shorten the intervals between bouts of tail display, increase the number of Fan beats in each bout and increase the number of bouts before entering Creep and attempting to transfer a spermatophore. Although the number of females present was also varied, these results could not have been caused by a response of males to changes in female density, as the number of females present was not changed *within* populations, while the differences *between* populations were controlled for in the regressions. The males may be increasing their investment of time and energy in display because they have to compete with a rival for the female's attention. In the smooth newt *T. vulgaris*, VERRELL (1984) found similar results, with males increasing the proportion of static display time spent Fanning when a second male was present. The frequency (Hz) of Fanning is unaffected by intrasexual competition, and males perhaps attempt to maintain a frequency which optimizes the efficiency of transfer of pheromone to the female.

These results suggest that *T. cristatus* males are selected to raise their investment in displays and produce more intense displays when there is competition for mates. Intrasexual competition has been shown to increase the frequency, intensity, duration or complexity of visual, olfactory, tactile or acoustic displays throughout the animal kingdom (e.g. insects: ALEXANDER 1975; GREENFIELD & SHAW 1983; fishes: FARR 1980; birds: BRADBURY & GIBSON 1983; frogs: GREEN 1990). Many authors have assumed that these responses to competitors increase a male's ability to obtain mates at the expense of increased costs, especially energetic expenditure. The energetic cost of display may well be significant in *T. cristatus*, because males appear to be under energetic limits (see below), and further energy spent displaying to one female is likely to reduce a male's capacity to display to a second. In nature, males occupy display positions in a lek that are visited by females (ZUIDERWIJK & SPARREBOOM 1986), and in some cases males may be visited by different females in quick succession. In *T. vulgaris*, females prefer to mate with males that have a higher dorsal crest, and in the laboratory a male's crest height is limited by foraging intake over the previous 6 days (GREEN *in press*). If this is the case for *T. cristatus*, spending energy during display may reduce a male's ability to develop a more attractive crest. Alternatively, it may reduce the size of fat stores essential for survival over the winter hibernation period (VERRELL *et al.* 1986).

In the absence of competitors, males may lower their investment in displays to reduce costs in currencies other than energetic expenditure. *T. cristatus* males may do so to save time if there is a chance of mating successively with more than one female, or a risk that a male may lose contact with a potential mate by displaying for so long that the female needs to retire to breathe at the surface. An alternative currency is predation risk (GREEN 1990), and by fatiguing males, intense displays may increase their vulnerability to predators.

GREEN (1989) observed three male *T. cristatus* who attempted to transfer a spermatophore to a female before conducting any static display. That male *T. cristatus* are selected to display more intensely to attract a mate when there are competing males present may explain why this attempted quick mating strategy has not been observed in the presence of a rival male.

### Evidence of Energetic Constraints

I have found considerable evidence to suggest that male *T. cristatus* are under energetic constraints during static display. There is evidence that fatigue limits the frequency (Hz) of their Fanning, the length (s) of courtship bouts and the speed ( $\text{min}^{-1}$ ) with which bouts are repeated. Fanning has a lower frequency in longer bouts because Fan beats get progressively slower as a bout progresses. As a courtship session continues, Fan bouts get shorter with fewer beats and males pause for longer between bouts. Males that use more bouts in a session also use longer intervals between them. As a male repeatedly reverts to courtship over several hours of observations, the peak bout from each session becomes shorter, with fewer beats, as time goes on.

Most of these effects are only firmly established for males displaying in the presence of a second male. Males court more intensely under these conditions, and therefore will become fatigued faster. If the reduction in bout lengths and increase in inter-bout intervals over time in the male display were caused by some motivational effect, we would predict the opposite result, i.e. that these effects would be weaker in the presence of a competing, second male. The decline in frequency (Hz) of Fanning within a bout is a strong effect even in the absence of other males, and this is not surprising since frequency is not affected by competition and its decline has been demonstrated only in long bouts with at least nine Fan beats which represent only 13 % of all bouts observed (GREEN 1989). Only the median length of bouts was increased by competition, not the maximum length.

Lashes are a rapid display only present in 15 % of bouts, and likely to be energetically costly (GREEN 1989). The fact that there is an increase in the frequency of Lashes as a courtship session proceeds cannot be explained by energetic constraints, although this increase in frequency may partially cause the increase in the duration of inter-bout intervals during a session. Lashes may be used to counter habituation or sensory adaptation of the female to Fanning, which will become more of a problem in later bouts.

During courtship, males are not able to breathe at the water surface and are therefore displaying with a limited supply of oxygen and a restricted potential for aerobic respiration. Hence, they are particularly likely to be under energetic constraints during courtship. However, some oxygen is likely to be taken up across the skin from the water (BANNIKOV 1948; SPURWAY & HALDANE 1953; CZOPEK 1959; ULTSCH 1976). One possible interpretation of the expulsion of air bubbles from the mouth of males observed during courtship (guffing, GREEN 1989) is that males are advertising their ability to maintain active courtship on a limited supply of oxygen by expelling gas from their lungs as a visual signal to the female. During this study a male was occasionally observed to break off static



display and breathe at the surface, bringing courtship to an end. This was not necessarily caused by an acute oxygen debt as males were observed nine times as often to terminate display without breathing. Thus males may withdraw for other reasons and then breathe to top up oxygen supplies even when these are not critically low (see HALLIDAY & SWEATMAN 1976). HALLIDAY (1977b) found that increasing the concentration of oxygen in the water and the air above it allowed male *T. vulgaris* to court for longer without breathing and to increase the percentage of static display time spent Fanning. Male *Triturus* may also rely on anaerobic respiration during courtship. Males of the red-spotted newt *Notophthalmus viridescens* are also unable to breathe at the surface while courting and increase their dependence on anaerobic metabolism when deprived of air (BENNETT & LICHT 1974).

There are trade-offs between the rate and duration of exertion during Fanning, with longer Fan bouts having a lower frequency of beating, and longer sessions having longer inter-bout intervals and therefore a lower percentage of time spent Fanning. Similar trade-offs have been found between the rate and duration of advertisement calls in the gray treefrog *Hyla versicolor* (WELLS & TAIGEN 1986). *H. versicolor* responds to vocal competition by increasing the duration of calls but decreasing the rate. Males producing long calls at slow rates also call for significantly fewer h per night than males in the same chorus producing shorter calls at higher rates. WELLS & TAIGEN argued that calling in *H. versicolor* is under energetic constraints, and males free from competition give shorter, less attractive calls so as to increase stamina and call for longer, while competing males give more attractive calls at the expense of stamina. Great tits *Parus major* singing during the dawn chorus have been observed to systemically decrease the percentage of time spent singing as a bout of singing proceeds (LAMBRECHTS & DHONDT 1988). This has been taken as evidence for neuromuscular exhaustion (but see WEARY et al. 1988; LAMBRECHTS 1988).

In order to confirm the existence of energetic constraints in the courtship of male *T. cristatus*, it would be desirable to demonstrate an effect of changing the oxygen content of the air and/or the water on the temporal dynamics of courtship, or to demonstrate a dependence on anaerobic metabolism by looking for a progressive accumulation of lactate during courtship.

### Courtship and Sexual Selection

The length and complexity of the sexual display of the male *T. cristatus* appears to far exceed the demands of passing a spermatophore between the sexes. This display has probably evolved in response to female preferences for mates with intense displays.

The selective forces which produce and maintain such female preferences remain uncertain. Male *T. cristatus* do not provide females with ecological benefits, such as paternal care or oviposition sites, that could be correlated with display. There are several ways in theory in which female preferences may be selected, but insufficient empirical data to draw any general conclusions (HEISLER et al. 1987; KIRKPATRICK 1987). However, the evidence that there are energetic constraints on the frequency (Hz) and length of Fan bouts and the duration of

inter-bout intervals is of great interest here. Static display intensity and duration appears to be an honest indicator of a male's ability to endure prolonged energetic expenditure. If this ability during courtship correlates with general vigour (e.g. ability to escape from predators; ability to capture food; parasite load) which shows genetic heritability, females may gain direct genetic benefits for their offspring by preferring males with longer and more intense displays. This is consistent with 'viability indicator' models of intersexual selection [e.g. ZAHAVI's theory (1975, 1977; WEST-EBERHARD 1979; ANDERSSON 1986; POMIANKOWSKI 1987) or HAMILTON & ZUK's theory (1982; KIRKPATRICK 1986)].

Viability-indicator theories are only one of several possible explanations for the evolution of female preferences for intense displays. Alternatives include a self-reinforcing Fisher runaway, intrinsic biases, selection of females to avoid hybridization with other species or selection on females to minimize the costs of finding a mate. These could still select for males to produce displays according to their physiological limits, but in an incidental fashion. This range of possibilities illustrates that it is not possible to establish how female preferences evolved by studying their effects on male traits (KIRKPATRICK 1987).

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