



# Survival regression analysis: a powerful tool for evaluating fighting and assessment

JORDI MOYA-LARAÑO\*† & DAVID H. WISE†

\*Unitat de Zoologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma de Barcelona

†Department of Entomology, University of Kentucky

(Received 6 May 1999; initial acceptance 22 July 1999;  
final acceptance 28 February 2000; MS. number: A8496R)

Theoretical models of animal contests frequently generate predictions about how asymmetries (e.g. differences in size, residence status) between contestants affect fight duration. Linear regression and nonparametric correlation analyses are commonly used to test the fit of data to such models. We show how survival regression analysis (SRA) is a powerful technique for studying the effect of asymmetries on the duration of contests. SRA, which is under-utilized by students of animal behaviour, offers several advantages over more frequently used procedures. It provides unbiased parameter estimates even when including censored data (i.e. results of contests that have not ended at the time when observations are stopped). The analysis of hazard functions, which is a component of SRA, is an easy way to test for consistency with predictions of the sequential assessment game model. These and other advantages of SRA are illustrated by using SRA and more conventional methods to analyse the effect of asymmetries on contest duration for encounters between female Mediterranean tarantulas, *Lycosa tarentula* (L.). It is hoped that this example of the advantages of SRA will encourage more widespread use of this powerful technique.

© 2000 The Association for the Study of Animal Behaviour

Game theoretical models of animal contests often make predictions about the duration of fights (e.g. Maynard Smith 1974; Maynard Smith & Parker 1976; Enquist & Leimar 1983; Leimar & Enquist 1984; Payne & Pagel 1997). For example, the sequential assessment game model (Enquist & Leimar 1983, 1987, 1990; Leimar & Enquist 1984), which assumes that animals sample each other's fighting ability as the fight progresses, predicts that: (1) the smaller the difference in relative fighting ability, the longer the duration of contests; (2) variability in contest duration increases as relative fighting ability decreases; and (3) when the owner of a resource loses a dispute, the contest will be longer than when the owner wins the fight.

Consistency with predictions about the duration of animal contests made by game theory models such as the sequential assessment game are usually evaluated by comparing the duration of fights between groups defined by a particular asymmetry (e.g. Riechert 1982; Verrel 1986; Crowley et al. 1988; Englund & Olsson 1990; Faber & Baylis 1993; DiMarco & Hanlon 1997; Hack et al. 1997), or by employing standard correlation and regression

techniques (e.g. Austad 1983; Verrel 1986; Englund & Olsson 1990; Enquist et al. 1990; Leimar et al. 1991; Olsson 1992; Marden & Rollins 1994; DiMarco & Hanlon 1997; Hack et al. 1997; Tobias 1997; Ladich 1998; Neat et al. 1998). Survival regression analysis (SRA) is a more powerful technique, but one rarely used by ethologists, for exploring how asymmetries may influence the duration of contests. In this paper we illustrate several features and major advantages of SRA.

Contrary to linear regression, SRA allows the inclusion of censored data (i.e. cases in which the contest did not end). This feature of SRA increases sample size without introducing bias in estimating the influence of asymmetries on contest duration. The analysis of hazard functions, a component of SRA, yields more information than a simple analysis of contest duration, because analysis of hazard functions reveals the pattern of change over time in the probability that the contest will end. Like other regression techniques, SRA permits testing for interactions between categorical and continuous variables in how they affect contest duration. Also, like other regression techniques, SRA yields standard errors of the regression parameters, allowing statistical comparison of parameters between different treatment groups and between studies.

Correspondence and present address: J. Moya-Laraño, Department of Entomology, S-225 Ag Sci Building-North, University of Kentucky, Lexington, KY 40546-0091, U.S.A. (email: [jmoya2@pop.uky.edu](mailto:jmoya2@pop.uky.edu)).

## SURVIVAL REGRESSION ANALYSIS

SRA has been widely used in the medical and social sciences (Allison 1995). Use of SRA in animal behavioural sciences has increased slightly in recent years (Haccou & Hemerik 1985; Muenchow 1986; Rhine et al. 1988; Haccou et al. 1991; van Alphen 1993; Eggert & Sakaluk 1994; van Roermund et al. 1994; Ormel et al. 1995; Moya-Laraño et al. 1996), but it is still under-utilized, perhaps due to its relative complexity. Although SRA was originally developed to analyse effects of different treatments on the time to death of patients, SRA can be used for studying 'the time to the occurrence of any event' ( $T$ ) (Allison 1995). The 'time until the end of a contest' will be our focus. Our explanation of SRA is based on Allison (1984, 1995). Other general references on the technique are Cox (1972), Kalbfleisch & Prentice (1980), Lawless (1982), Cox & Oakes (1984), SAS Institute (1990), Lee (1992), Kumar & Klefsjö (1994) and Klein & Moeschberger (1997). A few examples related specifically to analysing animal behaviour are Haccou & Hemerik (1985), Muenchow (1986), Haccou et al. (1991), Haccou & Meelis (1992) and Fox (1993). Some statistical packages that include SRA procedures are BMDP, JMP, SAS, SPSS, STATA, STATISTICA and SYSTAT. Analyses in this paper have been performed with SAS (SAS Institute 1990), except for hazard functions, which were estimated with STATISTICA (Statsoft 1995).

SRA can be performed with several models, which are defined by their ability to include 'censored data'. 'Right-censored' data includes cases in which the event under study has not occurred by the end of the observation period, which is often the case for studies reporting contest duration (e.g. Harvey & Corbet 1986; DiMarco & Hanlon 1997). In such situations the use of SRA is more accurate than linear regression (Allison 1995).

SRA can be accomplished using either parametric accelerated failure time models or the nonparametric Cox proportional hazards regression model (Cox 1972). As shown below, accelerated failure time models are very useful for studying contest duration because they allow analysis of the hazard function. For this reason, this paper focuses on accelerated failure time models only.

## SRA AND MEDITERRANEAN TARANTULA FIGHTS

In a study of territoriality in the Mediterranean tarantula, *Lycosa tarentula* (L.) (J. Moya-Laraño, J. M. Orta-Ocaña, J. A. Barrientos, C. Bach & D. H. Wise, unpublished data), 45 encounters between adult females were staged in the field. A spider (the intruder) was introduced into the territory of another spider (the resident) and the contest duration, behavioural patterns and outcome were recorded. Each contest ended when the loser ran away or was killed by the winner. Observations stopped after 60 min, at which time two contests had not ended (censored data). The carapace width of each spider was measured at the end of the contest.

Below we use these data on *L. tarentula* contests to illustrate the advantages of using SRA in determining whether or not data on contest duration fit predictions of

the sequential assessment game model. Before testing three of the model's predictions, we briefly describe the accelerated failure time models and outline the properties of the model that best describe the *L. tarentula* data.

When analysing data by means of ordinary (i.e. classic) least-squares regression, the dependent variable must fit a normal distribution. Similarly, when using accelerated failure time models of SRA, the distribution of the time to the occurrence of an event ( $T$ ) must fit a particular survival distribution. One typically selects from several standard survival distributions, some of which are simply particular cases of a general family of distributions (e.g. Weibull, exponential, gamma, log-logistic, log-normal, Gompertz; Allison 1995). The survival distribution that best fits the data will be the accelerated failure time model that will give the best unbiased estimators for the effects of the independent variables on  $T$ . Although both graphical and numerical methods exist for fitting survival distributions, the details of these methods go far beyond the scope of this paper (see Allison 1995, pp. 88–97). Applying the numerical method, we determined that the distribution of contest duration in the Mediterranean tarantula fits a Weibull distribution. The Weibull accelerated failure time model is defined by

$$\log T = \beta_0 + \beta_1 x_1 + \dots + \beta_k x_k + \sigma \varepsilon \quad (1)$$

$$\log h(t) = a \log t + \beta_0^* + \beta_1^* x_1 + \dots + \beta_k^* x_k \quad (2)$$

where  $T$  is contest duration and  $h(t)$  is the hazard function. The hazard rate is the conditional probability that the contest ends after any time  $T$ , within a small interval of time  $t + \Delta t$ , where  $T$  is greater than  $t$ . In the Weibull model the hazard is a function of time. This relationship is shown in equation (2), where  $a$  is a constant that relates the logarithm of time to the logarithm of the hazard. The hazard can accelerate, decelerate or not change with time. In equation (1) the parameter  $\varepsilon$  is a disturbance term analogous to the error term in least-squares regression, and  $\sigma$  is the scale parameter that, once estimated, is a measure of whether the hazard function accelerates or decelerates. The time to the event ( $T$ ) is observed, whereas the hazard,  $h(t)$ , is estimated from the model. Thus, equation (1) is a calculated regression model, whereas equation (2) is a theoretical relationship between the explanatory variables (i.e. the covariates  $x_1, x_2, \dots, x_k$ ) and the hazard function. If the hazard does not vary over time, the hazard would be exactly the inverse of contest duration (i.e.  $h(t) = 1/T$ ). Because the hazard is related to the duration of contests, equations (1) and (2) are related. After fitting the data to equation (1), one can estimate the effect of independent variables on  $h(t)$  (Allison 1995, page 73). The terms  $\beta_0$  and  $\beta_0^*$  are constants, and the terms  $\beta_1 x_1 + \dots + \beta_k x_k$  and  $\beta_1^* x_1 + \dots + \beta_k^* x_k$  estimate the effects of covariates on  $T$  and the hazard, respectively. If the  $\beta$ s are not significantly different from zero, they are removed from the model. Terms in an accelerated failure model are tested for statistical significance using a derivation of the maximum likelihood method that includes information on whether or not each case is censored. As in logistic regression (Hardy & Field 1998), the null hypothesis that

all coefficients are zero is tested using the log-likelihood ratio test. The statistic calculated in this test approaches a chi-square distribution with as many degrees of freedom as the number of covariates included in the model. The maximum likelihood procedure generates estimates of the parameters in equation (1):  $\beta_0, \beta_1 x_1 + \dots + \beta_k x_k$  and  $\sigma$ . The significance of each parameter is usually tested with the Wald test, which approaches a chi-square distribution with one degree of freedom.

### Testing Predictions of the Sequential Assessment Game Model

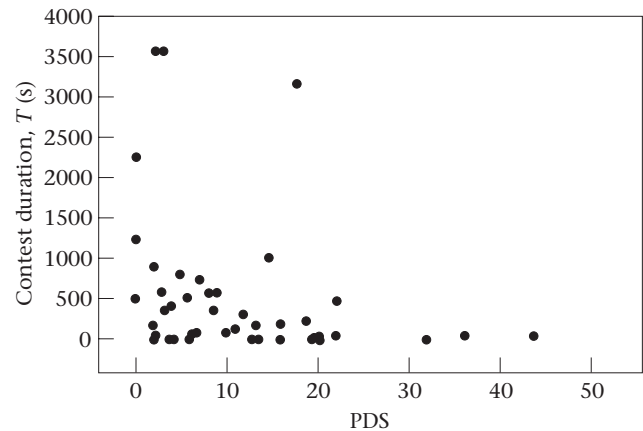
In this section we show the advantages of using SRA to examine the fit of the data to three predictions of the sequential assessment game model: (1) the smaller the relative fighting ability, the longer the duration of contests; (2) variability in contest duration increases as relative fighting ability decreases; and (3) contest duration will be longer when the owner of a territory loses a dispute.

#### Prediction (1): regression approach

Below we compare the output of different regression techniques in predicting the effect of relative fighting ability on contest duration, and show that as the number of censored data increases, this prediction is more accurate using SRA than conventional regression models. Because spider size is a good predictor of contest outcome in *L. tarentula* females (Fernández-Montraveta & Ortega 1990), we used the percentage difference in size as an index of relative fighting ability: percentage difference in size = [(carapace width of larger spider – carapace width of smaller spider) / (carapace width of smaller spider) × 100].

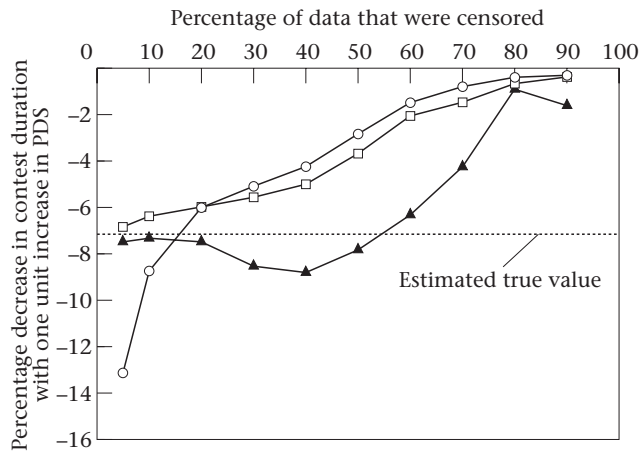
Researchers usually test whether relative fighting ability and  $T$  are negatively related by calculating the Spearman correlation coefficient (e.g. Verrel 1986; Englund & Olsson 1990; Enquist et al. 1990; Leimar et al. 1991; Olsson 1992). This statistic revealed a negative relationship with the *L. tarentula* data (Spearman rank correlation:  $r_s = -0.4030$ ,  $N=45$ ,  $P=0.006$ ; Fig. 1). Nevertheless, a regression technique is more potent, because, as we will show later, it reports the magnitude of the effect, which can be used to compare different groups and studies. Furthermore, a particular regression approach, SRA, is more robust with respect to censored data on contest duration.

Below we illustrate the higher robustness of SRA relative to other regression techniques when dealing with censored data. By ‘higher robustness’ we mean that as the number of censored data increases, parameter estimates, and therefore estimates of the magnitude of the effect, will remain more constant using SRA than conventional regression techniques. We ran a simulation in which the observed *L. tarentula* fights (Fig. 1) were artificially censored at successive intervals of 10% censored data. First we ran the simulation as if observations had been stopped when 90% of contests had ended (i.e. 10% of the data were censored). The time included in the censored data was the time of the last observation entering the 90%



**Figure 1.** Scatterplot showing a negative relationship between contest duration ( $T$ ) and the percentage difference in size (PDS), for 45 contests between *L. tarentula* (Moya-Laraño et al., unpublished data). Note that as PDS decreases, data points are further away from each other along the vertical ( $T$ ) axis, indicating an increasing variability in contest duration as relative fighting ability decreases (see text and Fig. 3).

threshold. Then the simulation was run as if observations had been stopped when 80% of contests had ended, and so on until 90% of the data were censored. For each percentage of censored data, we ran a Weibull accelerated failure time model (SRA model) and, for comparison purposes, two conventional regression techniques: ordinary least-squares regression (time log-transformed) and nonlinear regression (SAS Institute 1990; Sibly et al. 1990). Because these conventional regression techniques do not allow specification of which data are censored, all contests that continued beyond the simulated observation period were entered as having ended when the observation period ended. The percentage of change in contest duration explained by an increase of one unit in a continuous independent variable, hereafter called ‘effect’, is calculated as  $100(e^{\beta} - 1)$ . Figure 2 shows the negative effect of the percentage difference in size on  $T$  for the different models and the percentage of censored data for each. The effect of the percentage difference in size on  $T$  was statistically significant for the Weibull accelerated failure time model for simulations ranging from 5 to 60% censored data ( $P$  value range 0.001–0.026). Over this range of simulated censored data, the calculated statistical significance of the negative effect of the percentage difference in size on  $T$  was generally an order of magnitude less for the two conventional regression techniques ( $P$  value range: ordinary least-squares regression: 0.022–0.212; nonlinear regression: 0.015–0.131). Without censored data, an ordinary least-squares regression calculates the best, unbiased estimators (Allison 1995). Therefore, with two censored observations, the true value must lie somewhere between the prediction by the least-squares regression and the Weibull accelerated failure time model. This estimate of the true value is represented in Fig. 2 by a horizontal dotted line. For almost all percentages of censored data, the SRA Weibull accelerated failure time model yielded parameter values that were closer to the estimated true value than the conventional regression



**Figure 2.** Results of a simulation in which data on contest duration for *L. tarentula* were considered as censored at successive 10% intervals (i.e. as if observations had been stopped when 10, 20, 30%, etc. of contests had not ended). The percentage difference in size (PDS) between contestants is a measure of relative fighting ability and is defined in the text. The effect of PDS on contest duration was calculated as  $100(e^{\beta}-1)$ , where  $\beta$  is the regression coefficient of PDS in all regression models (see text for details). ▲: Weibull accelerated failure time model (the SRA model); □: ordinary least-squares regression model; ○: nonlinear regression model. The horizontal line shows the estimated true value of the effect, calculated as the mean of the effect estimated by the Weibull model and the effect estimated by the ordinary least-squares regression model with only two censored data points. The SRA Weibull accelerated failure time model was always closer to the true value than the non-SRA models (least-squares or linear regression). Note that with 60% of the data censored, the Weibull accelerated failure time model predicted an effect that was still very close to the estimated true value.

techniques. Even when the number of censored data was very low, nonlinear regression produced parameter estimates that were very far from the estimated true value.

Both SRA and conventional models reveal a negative relationship between relative fighting ability and contest duration, indicating that *L. tarentula* fights satisfy the first prediction of the sequential assessment game model. However, the SRA and the non-SRA models differ in the magnitudes of their estimates of how changes in percentage difference in size affect  $T$ , and they differ in their sensitivity to missing data. Because SRA is much more robust in estimating parameters, a researcher using SRA can still reliably estimate parameters while significantly decreasing observation effort.

#### Prediction (2): hazard function approach

The sequential assessment game model predicts that if animals are assessing their relative fighting ability during contests, variability in contest duration will increase as relative fighting ability decreases. In a graph of  $T$  (vertical axis) versus percentage difference in size (horizontal axis) (Fig. 1), this pattern appears as a trend in which, as the percentage difference in size, and thus relative fighting ability, decreases, data points tend to be more separated along the vertical axis. A similar pattern occurs in several

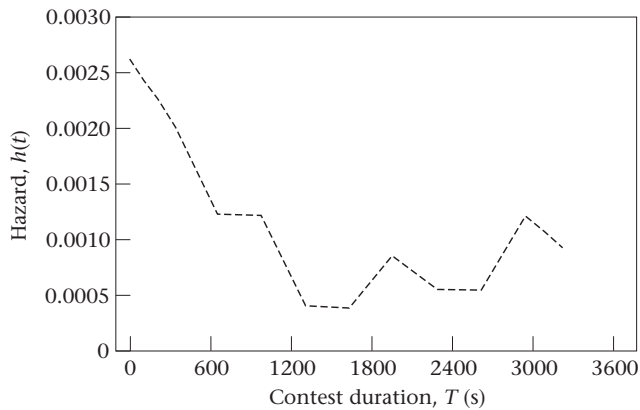
published graphs (Harvey & Corbet 1986; Wells 1988; Englund & Olsson 1990; Leimar et al. 1991; Olsson 1992; Jennions & Backwell 1996; DiMarco & Hanlon 1997; Hack et al. 1997). A quantitative test of how well such a pattern fits the prediction of the sequential assessment game is usually performed by pooling contests of similar relative fighting ability into groups (Englund & Olsson 1990; DiMarco & Hanlon 1997). Spearman rank correlation is then used to compare the standard deviation of  $T$  for each group with its rank based upon relative fighting ability. We pooled *L. tarentula* fights into nine groups of five fights each, and found that the standard deviation of contest duration was negatively correlated with the percentage difference in size (Spearman rank correlation:  $r_s = -0.7333$ ,  $N=9$ ,  $P=0.025$ ), as predicted by the sequential assessment game model.

SRA permits a quantitative exploration of the same pattern simply by measuring the acceleration or deceleration of the hazard function,  $h(t)$ . An accelerating  $h(t)$  means that the variability in time to the end of the contest is decreasing as time elapses, whereas a decelerating  $h(t)$  means that such variability increases with time. After showing that contest duration increases as relative fighting ability decreases, one can next determine whether variability in  $T$  increases with decreasing relative fighting ability by showing that  $h(t)$  decreases with time. Therefore, if the percentage difference in size explains  $h(t)$  and the latter decreases as time elapses, one can conclude that the smaller the percentage difference in size, the larger the variability in  $T$ , as predicted by the sequential assessment game model. The test of whether  $h(t)$  accelerates or decelerates as time elapses is provided by the scale parameter,  $\sigma$ , in the Weibull accelerated failure time model. SAS reports a statistic that tests for the null hypothesis that  $\sigma$  equals 1 (Cox & Oakes 1984); a derivation of the Wald test can also be used (SAS Institute 1990). If the data fit a Weibull function,  $\sigma$  greater than 1 would indicate that the hazard decreases with time.

Fitting the duration of *L. tarentula* contests to the Weibull distribution resulted in a scale parameter that was significantly greater than 1 ( $\sigma=1.75$ ; Wald test  $\chi^2_1=12.9$ ,  $P=0.0003$ ), indicating that the hazard decreases with time (Fig. 3). Thus, the variance in  $T$  increases over time, and because the percentage difference in size was negatively correlated with contest duration in *L. tarentula*, we can conclude that the pattern is consistent with the second prediction of the sequential assessment game model (i.e. variability in  $T$  increases as fighting ability decreases).

Therefore, survival analysis provides a statistic to test objectively whether the variability in contest duration increases as fighting ability decreases. One could also use the more conventional non-SRA approaches. The two main advantages of using SRA versus comparing groups with Spearman correlation are that: (1) the researcher avoids the step of grouping data, which is subjected to a potential lack of objectivity; and (2) SRA models are designed to incorporate censored data, so  $h(t)$  will be measured with less bias than calculating the standard deviation of  $T$  with censored data included in arbitrarily grouped contests.





**Figure 3.** Decelerating hazard function of the time to the end of the contest. In combination with a negative relationship between contest duration and the percentage difference in size, PDS (Fig. 1), a decelerating hazard function means that variability in contest duration decreases as PDS increases, one of the predictions of the sequential assessment game model (see text for details).

**Table 1.** Estimation of the effect of percentage difference in size (PDS) and residence asymmetries, and their interaction on contest duration ( $T$ ) of Mediterranean tarantula females using a Weibull SRA model

	$\chi^2_3$	$P$	Coefficient	SE	$P$ (Wald)
<b>Full model</b>	10.4	0.0158			
<b>Variable</b>					
Intercept ( $\beta_0$ )			7.54	0.75	0.0001
PDS			-0.08	0.03	0.0027
Residence			-0.98	0.48	0.0436
PDS $\times$ residence			-0.12	0.05	0.0236
Scale ( $\sigma$ )			1.48	0.18	0.0001

Only noncensored data were analysed ( $N=43$ ) because the categorical variable 'residence' was defined only if the contest had ended and a winner could be identified.

### Prediction (3): interaction terms

One goal in the study of animal fights is to separate effects of asymmetries that occur simultaneously (e.g. Waage 1988; Marden & Waage 1990). A powerful and efficient approach to this problem is to examine how asymmetries interact. Although most multivariate techniques allow the inclusion of interactions between variables, this is infrequently done when studying the effect of asymmetries on animal fights. SRA, like other statistical models, estimates parameters more accurately if interaction terms are included (Kumar & Klefsjö 1994). Below we illustrate this point with the *L. tarentula* data.

The sequential assessment game model predicts that fights in which the resident individual wins will be shorter than those in which the intruder wins. The residence asymmetry may interact with relative fighting ability in determining contest duration. In Table 1 we summarize the results of a complete analysis of the *L. tarentula* data in which we included, in a SRA Weibull accelerated failure time model, effects of the continuous independent variable, percentage difference in size, the categorical variable, residence, which took the value 1

when the resident spider won and 2 when the intruder won; and the interaction, percentage difference in size  $\times$  residence. All three effects were significant. The effect of the percentage difference in size on  $T$  was negative, as was shown earlier. The coefficient for residence was negative, indicating that when the intruder won (residence=2, the larger value), contest duration was shorter. This outcome is opposite to what the sequential assessment game model predicts. Because the interaction term was significant, we then ran two different models to reveal the nature of the interaction (Pedhazur 1973): one with the continuous independent variable (percentage difference in size) for only those contests in which the owner won, and another for those contests in which the intruder won. The percentage difference in size did not explain contest duration in those fights in which the resident won, but showed a highly significant and negative effect of relative fighting ability on contest duration when intruders won (J. Moya-Laraño et al., unpublished data).

### Comparing Coefficients Between Groups

The  $\beta$  coefficient for relative fighting ability can be a good measure of the value of the disputed resource if it accurately measures the relationship between relative fighting ability and  $T$ . The sequential assessment game model (Enquist & Leimar 1987; Leimar et al. 1991) predicts that animals will fight for a longer time when the value of the resource is higher. Therefore, we expect that the absolute value of  $\beta$  will be larger when the resource is of higher value, because the slope relating relative fighting ability to  $T$  should be steeper in fights for a more valuable resource. Reporting  $\beta$  coefficients along with their standard errors allows statistical comparison of an index of resource quality between groups, and between results of different empirical studies (Allison 1995, page 199). Such analyses can be very useful in comparative studies. Although ordinary least-squares regression could also be used for such comparisons, the advantage of SRA is that groups with different amounts of censored data can be compared more accurately.

### Sequential Assessment Game Model and Spider Fights

In our example using SRA to analyse contests between *L. tarentula*, we found clear agreement with two of the three predictions of the sequential assessment game model. The higher the relative fighting ability, the shorter the contest and the lower the variability in contest duration. The data were not consistent with the third prediction, that contests won by intruders should be longer. Never the less, the significant interaction between relative fighting ability and the residency asymmetries suggests that assessment of both asymmetries may occur. A more detailed discussion of this result can be found elsewhere (Moya-Laraño et al., unpublished data). These results are not conclusive proof that *L. tarentula* females

are playing the sequential assessment game; our findings are merely consistent with major predictions of the sequential assessment game model. The same results could be also consistent with other games (e.g. [Payne & Pagel 1997](#); [Payne 1998](#)). Additional research would be needed to more rigorously test the sequential assessment game model for the Mediterranean tarantula.

## CONCLUSIONS

Since SRA has been specially designed for the study of 'time-to-event' data, it is more accurate than other regression techniques, primarily because SRA accommodates censored data, allowing the researcher to reduce sampling effort while maintaining accuracy. In addition, the shape of the hazard function can be used to test one of the predictions of the sequential assessment game model. Like other techniques, SRA also allows inclusion of interactions and provides standard errors of the parameter estimations, allowing comparisons between different groups.

We hope that our example of the use of SRA will encourage other behavioural biologists to employ this powerful technique. SRA statistical packages are becoming more friendly and the publication of [Allison's \(1995\)](#) manual for the use of survival analysis in SAS has increased the accessibility of SRA to researchers.

## Acknowledgments

We thank D. Blumstein, G. Brown, G. Grether and R. Preziosi for helpful comments on the manuscript. We thank the Cabo Gata Natural Park for logistical support during the study that provided the data used as the basis for illustrating advantages of SRA. The Michelin group kindly allowed us to work on its property. A. Fulvo helped during the preparation of video recording and spider interactions. J.M. was supported by a scholarship from the Ministerio de Educación y Cultura of the Spanish Government (AP95 33906935). This work was partially funded by the ISC Programme of the European Union (Contract No. CI1\*-CT94-0099). This is Publication No. 98-08-53 of the Kentucky Agricultural Experiment Station.

## References

- Allison, P. D.** 1984. *Event History Analysis: Regression for Longitudinal Event Data*. Beverly Hills: Sage Publications.
- Allison, P. D.** 1995. *Survival Analysis Using the SAS System*. Cary, North Carolina: SAS Institute.
- van Alphen, J. J. M.** 1993. Patch residence time and encounters with parasitised hosts: a reaction. *Netherlands Journal of Zoology*, **43**, 340–349.
- Austad, S. N.** 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Animal Behaviour*, **31**, 59–73.
- Cox, R. D.** 1972. Regression models and life-tables. *Journal of the Royal Statistical Society*, **2**, 187–202.
- Cox, R. D. & Oakes, D.** 1984. *Analysis of Survival Data*. London: Chapman & Hall.
- Crowley, P. H., Gillet, S. & Lawton, J. H.** 1988. Contests between larval damselflies: empirical steps towards a better ESS model. *Animal Behaviour*, **36**, 1496–1510.
- DiMarco, F. P. & Hanlon, R. T.** 1997. Agonistic behavior in the squid *Loligo plei* (Loliginidae, Teuthoidea): fighting tactics and the effects of size and resource value. *Ethology*, **103**, 89–108.
- Eggert, A. K. & Sakaluk, S. K.** 1994. Sexual cannibalism and its relation to male mating success in sagebrush crickets, *Cyphoderris strepitans* (Haglidæ: Orthoptera). *Animal Behaviour*, **47**, 1171–1177.
- Englund, G. & Olsson, T. I.** 1990. Fighting and assessment in the net-spinning caddis larva *Arctopsysche ladogensis*: a test of the sequential assessment game. *Animal Behaviour*, **39**, 55–62.
- Enquist, M. & Leimar, O.** 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O.** 1987. Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, **127**, 187–205.
- Enquist, M. & Leimar, O.** 1990. The evolution of fatal fighting. *Animal Behaviour*, **39**, 1–9.
- Enquist, M., Leimar, O., Ljunberg, T., Mallner, Y. & Segerdahl, N.** 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **40**, 1–14.
- Faber, D. B. & Baylis, J. R.** 1993. Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). *Animal Behaviour*, **45**, 289–299.
- Fernández-Montraveta, C. & Ortega, J.** 1990. El comportamiento agonístico de hembras adultas de *Lycosa tarentula fasciventris* (Araneae, Lycosidae). *Journal of Arachnology*, **18**, 49–58.
- Fox, G. A.** 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. In: *Design and Analysis of Ecological Experiments* (Ed. by S. M. Scheiner & J. Gurevitch), pp. 253–289. New York: Chapman & Hall.
- Haccou, P. & Hemerik, P.** 1985. The influence of larval dispersal in the cinnabar moth (*Tyria jacobaeae*) on predation by the red wood ant (*Formica polyctena*): an analysis based on the proportional hazards model. *Journal of Animal Ecology*, **54**, 755–769.
- Haccou, P. & Meelis, E.** 1992. *Statistical Analysis of Behavioural Data: an Approach Based on Time-structured Models*. Oxford: Oxford University Press.
- Haccou, P., De Vlas, S. J., van Alphen, J. J. M. & Visser, M. E.** 1991. Information processing by foragers: effects of intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. *Journal of Animal Ecology*, **60**, 93–106.
- Hack, M. A., Thompson, D. J. & Fernandes, D. M.** 1997. Fighting in males of the autumn spider, *Metellina segmentata*: effects of relative body size, prior residency and female value on contest outcome and duration. *Ethology*, **103**, 488–498.
- Hardy, I. C. W. & Field, S. A.** 1998. Logistic regression of animal contests. *Animal Behaviour*, **56**, 787–792.
- Harvey, I. F. & Corbet, P. S.** 1986. Territorial interactions between larva of the dragonfly *Pyrhosoma nymphula*: outcome of encounters. *Animal Behaviour*, **34**, 1550–1561.
- Jennions, M. D. & Backwell, P. R. Y.** 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society*, **57**, 293–306.
- Kalbfleisch, R. L. & Prentice, J. D.** 1980. *The Statistical Analysis of Failure Time Data*. New York: J. Wiley.
- Klein, J. P. & Moeschberger, M. L.** 1997. *Survival Analysis: Techniques for Censored and Truncated Data*. New York: Springer.
- Kumar, D. & Klefsjö, B.** 1994. Proportional hazards model: a review. *Reliability Engineering and System Safety*, **44**, 177–188.
- Ladich, F. A.** 1998. Sound characteristics and outcome of contests in male croaking gouramis (Teleostei). *Ethology*, **104**, 517–529.
- Lawless, J. F.** 1982. *Statistical Models and Methods for Lifetime Data*. New York: J. Wiley.

- Lee, E. T. 1992. *Statistical Methods for Survival Data Analysis*. 2nd edn. New York: J. Wiley.
- Leimar, O. & Enquist, M. 1984. Effects of asymmetries in owner-intruder conflicts. *Journal of Theoretical Biology*, **111**, 475–491.
- Leimar, O., Austad, S. & Enquist, M. 1991. A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. *Evolution*, **45**, 862–874.
- Marden, J. H. & Rollins, R. A. 1994. Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Animal Behaviour*, **48**, 1023–1030.
- Marden, J. H. & Waage, J. K. 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Animal Behaviour*, **39**, 954–959.
- Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, **47**, 209–221.
- Maynard Smith, J. & Parker, G. A. 1976. The logic of asymmetric contests. *Animal Behaviour*, **24**, 159–175.
- Moya-Laraño, J., Orta-Ocaña, J. M., Barrientos, J. A. & Cases, A. 1996. Dynamics of a population of burrowing wolf spiders. Is there any competition? *Revue Suisse de Zoologie, hors série*, 491–499.
- Muenchow, G. 1986. Ecological use of failure time analysis. *Ecology*, **67**, 246–250.
- Neat, F. C., Huntingford, F. A. & Beveridge-Malcolm, M. C. 1998. Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. *Animal Behaviour*, **55**, 883–891.
- Olsson, M. 1992. Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Animal Behaviour*, **44**, 386–388.
- Ormel, G. J., Gort, G., van Alebeek, F. A. N. 1995. Analysing host location in *Uscana lariophaga* (Hymenoptera: Trichogrammatidae), an egg parasitoid of bruchids (Coleoptera: Bruchidae), using Cox's proportional hazards model. *Bulletin of Entomological Research*, **85**, 113–123.
- Payne, R. J. 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour*, **56**, 651–662.
- Payne, R. J. & Pagel, M. 1997. Why do animals repeat displays? *Animal Behaviour*, **54**, 109–119.
- Pedhazur, E. J. 1973. *Multiple Regression in Behavioral Research. Explanation and Prediction*. New York: Holt Rinehart & Winston.
- Rhine, R. J., Wasser, S. K. & Norton, G. W. 1988. Eight-year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. *American Journal of Primatology*, **16**, 199–212.
- Riechert, S. E. 1982. Spider interaction strategies: communication vs. coercion. In: *Spider Communication: Mechanisms and Ecological Significance* (Ed. by P. N. Witt & J. S. Rovner), pp. 281–315. Princeton, New Jersey: Princeton University Press.
- van Roermund, H. J. W., Hemerik, L. & van Lenteren, J. C. 1994. Influence of intrapatch experiences and temperature on the time allocation of the whitefly parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). *Journal of Insect Behavior*, **7**, 483–501.
- SAS Institute 1990. *User's Guide*. Cary, North Carolina: SAS Institute.
- Sibly, R. M., Nott, M. R. & Fletcher, D. J. 1990. Splitting behaviour into bouts. *Animal Behaviour*, **39**, 63–69.
- Statsoft. 1995. *STATISTICA Vol. III: STATISTICS II*. Tulsa, Oklahoma: Statsoft.
- Tobias, J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Animal Behaviour*, **54**, 9–21.
- Verrel, P. A. 1986. Wrestling in the red-spotted newt (*Notophthalmus viridescens*): resource value and contestant asymmetry determine contest duration and outcome. *Animal Behaviour*, **34**, 398–402.
- Waage, J. K. 1988. Confusion over residency and the escalation of damselfly territorial disputes. *Animal Behaviour*, **36**, 586–595.
- Wells, M. S. 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. *Animal Behaviour*, **36**, 321–326.