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DOI: <https://doi.org/10.1139/cjz-79-5-895>

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ZORA URL: <https://doi.org/10.5167/uzh-548>

Journal Article

Published Version

Originally published at:

Anholt, B R; Vorburger, C; Knaus, P (2001). Mark–recapture estimates of daily survival rates of two damselflies (*Coenagrion puella* and *Ischnura elegans*). *Canadian Journal of Zoology*, 79(5):895-899.

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Mark-recapture estimates of daily survival rates of two damselflies (*Coenagrion puella* and *Ischnura elegans*)

Bradley R. Anholt, Christoph Vorburger, and Peter Knaus

Abstract: Male-biased operational sex ratios are very common in sexually mature dragonflies. These may be due to differential survival or differences in time spent at the breeding site by the sexes. Because most studies are carried out at the breeding site, these two processes can be measured as survival rates or recapture rates using modern capture-mark-recapture methods. We marked 66 female and 233 male *Coenagrion puella*, and 137 female and 347 male *Ischnura elegans* during three capture periods spread over 18 days. Each time an animal was recaptured it was re-marked so that the capture history of any captured animal could be readily identified. We recaptured 131 *C. puella* and 55 *I. elegans* at least once. We used the Cormack-Jolly-Seber model to estimate the daily probability of survival and recapture. The probability of recapture was, on average, more than three times higher for male *C. puella* (0.489) than females (0.133) with significant day to day variation. The daily probability of survival did not differ significantly between the sexes (0.860), with no significant variation among days. In contrast, in *I. elegans* the probability of recapture did not differ between the sexes (0.139 for the first 5 days; between 0.032 and 0.287 for the final 3 days), but the daily probability of surviving was much higher for males (0.812) than for females (0.579). Assuming that the sex ratio was unity at sexual maturity, the recapture and survival rates predicted well the sex ratio of the sample of *C. puella* but predicted more males than were observed in the sample of *I. elegans*. This suggests that male *I. elegans* may suffer higher mortality than females in the immature stage.

Résumé : Un rapport mâles : femelles effectif supérieur à 1 est fréquent chez les libellules qui ont atteint leur maturité sexuelle, peut-être à cause d'un taux de survie différentiel ou de différences dans le temps passé au site de reproduction par les deux sexes. Comme la plupart des études se font au site de reproduction, ces deux processus peuvent être mesurés par estimation du taux de survie ou du taux de recapture à l'aide d'une version récente de la méthode capture-marquage-recapture. Nous avons marqué 66 femelles et 233 mâles de *Coenagrion puella* et 137 femelles et 347 mâles d'*Ischnura elegans* au cours de trois périodes de capture s'étendant sur 18 jours. Chaque fois qu'une libellule était capturée, elle était marquée de nouveau de façon à ce que la séquence des captures de chaque insecte puisse être déterminée facilement. Nous avons recapturé 131 *C. puella* et 55 *I. elegans* au moins une fois. Nous avons utilisé le modèle de Cormack-Jolly-Seber pour estimer la probabilité quotidienne de survie et de recapture. La probabilité de recapture s'est avérée, en moyenne, trois fois plus élevée chez les mâles (0,489) que chez les femelles (0,133) de *C. puella* avec une variation significative d'une journée à l'autre. La probabilité de survie ne différait pas significativement entre les mâles et les femelles (0,860) et la variation d'une journée à l'autre n'était pas significative. En revanche, la probabilité de recapture ne différait pas chez les mâles et les femelles d'*I. elegans* (0,139 au cours des 5 premiers jours et entre 0,032 et 0,287 au cours des 3 derniers jours), mais la probabilité quotidienne de survie était beaucoup plus élevée chez les mâles (0,812) que chez les femelles (0,579). En supposant des rapports mâles : femelles égaux à la maturité sexuelle, les taux de recapture et de survie ont été de bons indicateurs du rapport mâles : femelles chez *C. puella*, mais ils ont prédit un nombre de mâles plus grand que le nombre observé chez *I. elegans*. Les mâles d'*I. elegans* semblent donc subir une mortalité plus grande que celle des femelles au cours de la phase immature.

[Traduit par la Rédaction]

Introduction

For successful reproduction, females require resources to provision eggs, while males require resources to find and attract mates. However, the acquisition of resources often entails a significant cost by increasing the risk of predation

(reviewed in Sih 1987; Lima and Dill 1990; Lima 1998). When the fitness advantage of additional resources differs between the sexes, we might expect to find differences in the mortality rates of males and females. Differences in mortality rates will shift the secondary sex ratio to favour the sex with lower mortality rates. Changes in the population

Received July 31, 2000. Accepted February 26, 2001. Published on the NRC Research Press Web site on May 8, 2001.

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sex ratio can have profound effects on the mating system (Emlen and Oring 1977). For example, if females are in very short supply, this can favour mate guarding, which will preclude other activities, including territorial defense.

In adults of nonterritorial species of Odonata, the sexes emerge at the same body mass, but at sexual maturity females are much heavier than males (Anholt et al. 1991). Most of this mass increase is associated with producing eggs (Corbet 1999). There is no advantage to large size in males because larger males do not generally have higher mating success (Fincke 1982; Anholt 1991, 1997; reviewed by Fincke et al. 1997). The mortality cost to females of gaining this additional mass may explain the male-biased sex ratio usually observed at the water's edge (Fincke et al. 1997; Corbet 1999). However, females normally spend less time at the water's edge and more time feeding (Banks and Thompson 1987; Anholt 1992), which would also lead to the operational sex ratio being male-biased. Further, because females are usually more cryptically coloured, they can be under-represented in a census (Anholt 1997). Because the probability of observing a previously marked animal is the product of its survival and recapture probabilities, simple resighting rates confound these two probabilities. When recapture rates are not 100%, minimum life-span (which is based on resighting) is a biased estimate. Often the assumption is made that the probability of recapture is 100% (e.g., Michiels and Dhondt 1989; Anholt 1991; Cordero 1995). Disentangling the probabilities of survival and detection can be accomplished by using modern implementations of the Cormack-Jolly-Seber (CJS) model for analyzing capture-mark-recapture data. These approaches fit estimates of both recapture and survival rates that minimize the residual deviance of the data (Lebreton et al. 1992). That is, they maximize the fit of the predicted resightings to the observed data in a way analogous to multiple regression. These methods also provide confidence limits on the estimates and a firm basis for testing hypotheses about differences in survival or recapture probabilities between groups.

In this paper we use data on survival and recapture of two common zygopterans with contrasting oviposition behaviour and patterns of sexually dimorphic mass gain to show that differences in observed sex ratio can be the result of either differential survival or recapture. We then go on to show how the survival rates can be used to generate hypotheses about survival rates at other points in the life cycle.

Material and methods

Study site and species

Our study area is located on the Irchel campus of the University of Zürich, Zürich, Switzerland. It includes three adjacent human-modified ponds that are almost fully surrounded by *Phragmites* reeds. The largest pond is $\sim 80 \times 20$ m, the smaller ponds are both about 10×10 m. The sites are isolated from other ponds by about 350 m.

The two most common zygopteran species at the ponds are *Coenagrion puella* and *Ischnura elegans*. Male *C. puella* are bright blue, while the females are green, though, rarely, their coloration contains some blue. Males contact-guard after mating and accompany the females during egg laying in the "tandem" position. Provided they survive long enough, females will mate more than once. Male *I. elegans* are predominantly black. The thorax shows blue or

green stripes and the 8th abdominal segment appears as a bright blue "taillight." Although we could distinguish three female colour variants (a blue androchromous, a green, and a brown form) the data for each form were too sparse to analyze separately. Female *I. elegans* are not guarded when egg laying and in some studies females were found to mate only once (Rowe 1978; Fincke 1987), but other species of *Ischnura* have been observed to mate repeatedly in the laboratory (Cooper et al. 1996) and the field (Cordero et al. 1997).

Mark-recapture

We captured mature adult damselflies at the ponds with nets and marked them on their wings with permanent-ink pens. Every week we used a different mark and for every day of the week we used a different colour. Every captured animal could be readily classified as to the dates (if any) on which it had previously been caught and we could thereby reconstruct its capture history. We had three capture periods separated by several days spread over 18 days (June 19, 20, 21, 26, 27, 28, and 29 and July 4, 5, and 6). We obtained capture histories for 299 *C. puella* (66 females and 233 males) and 484 *I. elegans* (137 females and 347 males). On the last capture day (July 6) we sacrificed 10 males and 10 females of each species and weighed them in the laboratory (± 0.1 mg).

We first tested the goodness of fit of the data to the CJS model using a parametric bootstrap of the saturated model as implemented in MARK version 1.0. (White and Burnham 1999). We then estimated the probability of survival and recapture from the capture histories with maximum likelihood for the CJS model using MARK version 1.0. This gave identical results to SURGE 4 (Lebreton et al. 1992). We began with a fully parameterized model with separate survival and recapture estimates for each day for each species' sex combination. We assumed constant daily survival between June 21 and 26 and between June 29 and July 4 because of a zero probability of recapture. We then simplified the models by constraining recapture estimates to be equal across adjacent days within a capture period and then between the sexes within species. We retained a simplification when this reduced Akaike's Information Criterion (AIC) for the model. AIC has been shown to be more reliable in model selection than the likelihood-ratio test (G test) (Burnham et al. 1995).

Results

Mass

Female *C. puella* weighed more than twice as much as males (29.5 ± 6.3 vs. 14.5 ± 6.1 mg (mean $\pm$ SD); $t_{18} = 7.6$, $P < 0.0001$), while female *I. elegans* were only 50% heavier than males (22.5 ± 2.9 vs. 15.0 ± 4.5 mg; $t_{18} = 6.4$, $P < 0.0001$).

Recapture

The recapture data did not significantly deviate from the expectations of the CJS model for the two species. Indeed the data were closer to the expectation of the multinomial distribution that we would expect by chance ($P = 1.0$ for 1000 bootstrap replicates). Because the fit is so close, we have not used a quasi-likelihood parameter for adjusting AIC values or likelihood statistics.

For *C. puella* the overall probability of recapture was almost four times higher for males than for females (49.0 ± 3.03 vs. $13.1 \pm 3.80\%$). However, recapture probabilities for *C. puella* estimated from the minimum adequate model were highly variable among days, and the pattern of variation was not similar between the sexes (Table 1) For males, reducing

Table 1. Maximum-likelihood estimates of recapture probability from the minimum adequate model of recapturing surviving individuals.

	Dates	Recapture probability	Standard error	Lower 95% confidence limit	Upper 95% confidence limit
<i>Ischnura elegans</i>					
Males and females combined	June 20, 21, 26–29	0.139	0.023	0.010	0.190
	July 4	0.287	0.112	0.121	0.540
	July 5	0.032	0.019	0.010	0.099
	July 6	0.104	0.036	0.052	0.198
<i>Coenagrion puella</i>					
Females	June 20, 21	0	Fixed		
	June 26, 27	0.562	0.161	0.263	0.822
	June 28, 29	0.113	0.054	0.042	0.270
	July 4, 5, 6	0.038	0.028	0.009	0.147
Males	June 20	0.861	0.105	0.527	0.972
	June 21	0.159	0.052	0.081	0.290
	June 26–29	0.606	0.040	0.525	0.681
	July 4, 5, 6	0.374	0.049	0.283	0.473

the number of recapture parameters from 9 to 4 did not significantly reduce the fit of the model ($\chi^2_5 = 5.9$, $P = 0.32$), but a further reduction to a single recapture parameter did reduce the fit unacceptably ($\chi^2_3 = 44.5$, $P < 0.0001$). On 4 days, June 19, 20, and 28 and July 5, no female *C. puella* were recaptured at all. We fixed the recapture rate for June 19 and 20 to zero, fitted a single parameter to June 28 and 29 and another to July 4, 5, and 6 (Table 1). Fitting a single parameter to June 28 and 29 did not appreciably affect the fit of the data to the model ($\chi^2_1 < 0.01$, $P = 0.92$). The model could have been further simplified by fitting a single parameter to July 4 and 6 but these dates were not adjacent.

Overall, recapture rates for male and female *I. elegans* (12.2 and 11.6%, respectively) were similar to that of female *C. puella* and not significantly different from each other ($\chi^2_1 = 0.06$, $P = 0.81$). For *I. elegans*, recapture rates (males and females combined) were similar across the first two recapture periods ($\chi^2_5 = 9.9$, $P = 0.08$), but there was significant heterogeneity among the final 3 days ($\chi^2_2 = 15.5$, $P = 0.0004$) (Table 1).

Survival

The daily probability of survival in *C. puella* was 86.0%/day and did not differ between males and females ($\chi^2_1 = 0.2$, $P = 0.89$; Table 2) or among days ($\chi^2_6 = 7.4$, $P = 0.28$).

Daily probability of survival of male *I. elegans* was similar to that of *C. puella* and much higher than that of female *I. elegans* (81.2 vs. 57.9 %/day; $\chi^2_1 = 10.4$, $P = 0.0013$) (Table 2) The minimum adequate model did not include daily variation in survival rates, although there was considerable variation in the estimates among days ($\chi^2_{10} = 17.3$, $P = 0.07$).

Discussion

Although the sex ratio at birth is almost always unity (or very near) for diploid organisms, we frequently observe that the sex ratio at the breeding site deviates from unity. This is almost always the case with damselflies. There are two possible reasons why we captured more males than females in both species. It is possible that the sex ratio was unity but that females were harder to catch because of their cryptic

Table 2. Maximum-likelihood estimates of survival calculated from the minimum adequate model.

	Survival probability	Standard error	Lower 95% confidence limit	Upper 95% confidence limit
<i>I. elegans</i>				
Females	0.579	0.086	0.048	0.733
Males	0.812	0.031	0.743	0.865
<i>C. puella</i>	0.860	0.014	0.831	0.885

coloration, less conspicuous behaviour, or their habitat choice. If this were the case we would expect to find higher recapture rates in males. This was true for one species, *C. puella*, in which the difference in coloration is indeed more pronounced. However, we also captured more male than female *I. elegans*, where recapture rates were similar. In this case, females had much lower survival rates. Thus, the cause of the observed male-biased sex ratio differs between species. The use of resighting rates that do not distinguish between survival and recapture probabilities would not have resolved this pattern and hence is clearly inappropriate.

Both male and female *I. elegans* are much darker than male *C. puella*. This darker coloration, combined with their more cryptic behaviour, may explain the lower recapture rates. A measure of encounter distances when sampling might provide the necessary estimates to test this hypothesis.

Daily survival rates were not time-dependent in either species, although the weather changed dramatically during the study period. On rainy days the damselflies do not appear at the water, but they seem to survive very well in protected places. Rain can reduce survival but it may need to be very heavy (e.g., Cordoba-Aguilar 1993).

Although our best estimates of survival of *C. puella* did not differ between the sexes, we observed females being captured by larval dragonflies several times during oviposition. Males always escaped. This may occur too infrequently to appreciably affect the relative survival rates of males and females. Alternatively, males may suffer higher mortality for some other reason associated with their bright coloration,

Table 3. Predicted $\left(\frac{\text{male life-span} \times P_{\text{recapture}}}{\text{female life-span} \times P_{\text{recapture}}} \right)$ versus observed sex ratios (males:females) in samples.

	Survival rate (day ⁻¹)	Life-span (days)	Recapture probability	Predicted sex ratio	Observed sex ratio	<i>P</i>
<i>I. elegans</i>				3.39	2.53	0.005
Males	0.824	4.68	0.119			
Females	0.608	1.55	0.106			
<i>C. puella</i>				3.40	3.53	0.84
Males	0.860	6.14	0.489			
Females	0.869	6.63	0.133			

Note: Estimates are taken from the simplest possible models and not the minimum adequate model that would include time effects on recapture. The sex ratio of the sample was compared with the predicted value using a binomial test.

which would compensate for the higher risk to females during oviposition. Female *I. elegans* oviposit alone, so any risk associated with this would be borne alone.

We can use our estimates of recapture and survival probabilities to predict the expected ratio of males to females that we captured for marking. The population sizes of males and females will be proportional to their expected life-span, which is equal to $P_{\text{survival}}/P_{\text{death}}$. Thus, the sex ratio of our samples should be the relative life-spans multiplied by the relative probabilities of capture (assuming that the probability of initial capture is the same as the probability of recapture). Because we only marked sexually mature individuals, this method also assumes that the sex ratio is unity at sexual maturity. The method predicted the observed sex ratio of *C. puella* very well, but the predicted sex ratio of *I. elegans* favoured males by about 34% more than that actually observed (binomial test, $P = 0.005$; Table 3), which argues that we should reject the assumption of equal survival to sexual maturity in *I. elegans*.

The sex ratio is usually very near unity at emergence in the Coenagrionidae, with a slight bias towards males (Corbet and Hoess 1998). One possible explanation for the smaller than expected proportion of males in *I. elegans* is that fewer males survive from emergence to sexual maturity. This is not what we would expect if there is a cost of resource acquisition in the pre-reproductive period, because females gain at least 50% more mass than males. Indirect survival estimates in other species of damselflies suggest that in the wild, immature females have lower survival to sexual maturity than males (Anholt 1991, 1997). However, this is by no means universally true (Cordoba-Aguilar 1993; Bennett and Mill 1995). Where measured, female *Ischnura* also tend to take a longer time to reach sexual maturity (Fincke 1987), which would also reduce survival to sexual maturity. Both of these effects are in the opposite direction to our observation of too few males. In the absence of predation, it appears that females generally live longer than males (Cordero 1994).

If female recapture probabilities are underestimated because of temporary emigration (Kendall et al. 1997) to an alternative feeding habitat, a higher proportion of males than observed would also be predicted. However, this should be detectable as a deviation from the expectation of multinomially distributed recapture frequencies, of which there is no suggestion in the data. There is no evidence that the probability

of recapturing an individual was affected by when it was last captured, which would be the case if females were using alternative habitats. Moreover, the effect of heterogeneous recapture probabilities on the estimates is usually small.

The probability of survival is a fundamental quantity in theories of ecology and evolution. To test these theories cleanly we need robust estimates of survival that are not biased by differences in recapture rates. In this study we have been able to show that survival of sexually mature male *I. verticalis* was higher than that of females but that male and female *C. puella* had similar survival rates. In both cases, however, the operational sex ratio was strongly male-biased. The difference lies in the recapture rates. We can use survival estimates to predict the expected life-span of the mature adult, and the population sex ratio, which will affect the expected number of matings. Finally, our failure to predict the sex ratio of captured animals using our estimates of survival and recapture suggests that male *I. verticalis* have lower survival than females prior to sexual maturity. This is unusual and merits further investigation.

Acknowledgements

We are grateful to Robby Stoks and two anonymous reviewers for careful comments on an earlier version of the manuscript. Data analysis and manuscript preparation were funded by a grant to B.R.A. from the Natural Sciences and Engineering Research Council of Canada.

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