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Factors Influencing Survival and Mark Retention in Postmetamorphic Boreal Chorus Frogs

Jennifer E. Swanson[1], Larissa L. Bailey[2], Erin Muths[3], and W. Chris Funk[4]

The ability to track individual animals is crucial in many field studies and often requires applying marks to captured individuals. Toe clipping has historically been a standard marking method for wild amphibian populations, but more recent marking methods include visual implant elastomer and photo identification. Unfortunately, few studies have investigated the influence and effectiveness of marking methods for recently metamorphosed individuals and as a result little is known about this life-history phase for most amphibians. Our focus was to explore survival probabilities, mark retention, and mark migration in postmetamorphic Boreal Chorus Frogs (*Psuedacris maculata*) in a laboratory setting. One hundred forty-seven individuals were assigned randomly to two treatment groups or a control group. Frogs in the first treatment group were marked with visual implant elastomer, while frogs in the second treatment group were toe clipped. Growth and mortality were recorded for one year and resulting data were analyzed using known-fate models in Program MARK. Model selection results suggested that survival probabilities of frogs varied with time and showed some variation among marking treatments. We found that frogs with multiple toes clipped on the same foot had lower survival probabilities than individuals in other treatments, but individuals can be marked by clipping a single toe on two different feet without any mark loss or negative survival effects. Individuals treated with visual implant elastomer had a mark migration rate of 4% and mark loss rate of 6%, and also showed very little negative survival impacts relative to control individuals.

DISTINGUISHING animals in the wild is imperative to the study of populations, especially those that are declining and thus targeted for conservation efforts (Perry et al., 2011). Such research often requires applying individual marks, particularly when a species or life-history phase tends to be difficult to detect or capture. In recent years these studies have become especially important in understanding declines that many amphibian populations are experiencing from factors such as disease, habitat loss, and global climate change (Lannoo, 2005). Unfortunately, work to understand or mitigate declines is often constrained by limited time or funding. As a result, projects focused on vulnerable amphibian species have been urged to emphasize research efforts on vital life-history stages in order to hasten the conservation of at-risk populations (Biek et al., 2002).

In the past, population dynamics were thought to depend largely upon the survival of premetamorphic life-history stages (Duellman, 1985; Berven, 1995; Alford and Richards, 1999). However, more recent work indicates that for many anurans the postmetamorphic life stage is actually the most essential in predicting and preventing further population decline (Biek et al., 2002). This supports the rationale that conservation will be most effective when survival of postmetamorphic life stages is central to management strategies (Conroy and Brook, 2003; Di Minin and Griffiths, 2011). Reliable marking techniques are critical to acquire accurate demographic information on vital postmetamorphic life-history stages and thus facilitate management success.

Traditionally, frogs have been marked by toe clipping, but recent concerns with this practice have raised ethical dilemmas that challenge scientists to better explore the possible adverse effects of toe clipping and examine alternative marking methods (McCarthy and Parris, 2004; Funk et al., 2005; Perry et at., 2011). In a recent review, Perry et al. (2011) found that 22% of studies that explored the physical and behavioral effects of toe clipping on amphibians and reptiles showed statistically significant negative effects. In frog species, the most notable effect of toe clipping was a reduction in the probability of recapture, a common behavioral response in many vertebrate species and one that is easily accommodated by models used to estimate population vital rates (Williams et al., 2002). Accordingly, some researchers argue that although no marking technique is ideal, for the bulk of amphibian species toe clipping causes less damage than other practices and it is necessary to provide scientific information that is imperative to managing threatened species (Funk et al., 2005). This moral dispute continues to promote more rigorous exploration of all marking techniques and their potential effects on the demographics of amphibian species (May, 2004; Perry et al., 2011).

Alternative marking methods include visual implant elastomer (VIE) and photo identification, but little is known about the effectiveness of these new procedures, especially for anurans. Some studies of adult anurans report that VIE can be visible 15 months after injection (Hoffmann et al., 2008; Campbell et al., 2009), but these studies did not address the potential effects of marking on demographic parameters such as survival or growth. In a short-term study, Moosman and Moosman (2006) showed no mortality and retention of all marks among VIE marked adult Wood Frogs (*Rana* [*Lithobates*] *sylvatica* [*sylvaticus*]), although 31% of marks migrated from the original injection location. To our knowledge, no previous anuran study has compared both

[1] Department of Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Delivery, Fort Collins, Colorado 80523; E-mail: jeswanson1@gmail.com. Send reprint requests to this address.
[2] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, Colorado 80523; E-mail: larissa.bailey@colostate.edu.
[3] U.S. Geological Survey Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80525; E-mail: muthse@usgs.gov.
[4] Department of Biology, Colorado State University, 1878 Campus Delivery, Fort Collins, Colorado 80523; E-mail: Chris.Funk@colostate.edu.
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short- and long-term survival, mark loss, and mark migration rates for different marking methods relative to unmarked individuals. This information about any marking method is critical because, ideally, such methods need to be retained long-term and meet assumptions common to most demographic analyses, namely, that: (1) marks are not lost nor are they overlooked or misidentified by the observer; and (2) there is no mark-induced reduction in survival probabilities.

This study provides new information about marking techniques for a species and life-history phase that is understudied. Basic demographic rates are lacking for all life stages of the Boreal Chorus Frog (*Psuedacris maculata*). This species' lifespan is unknown, but related species in the *triseriata* complex are thought to live 1–3 years with reproduction occurring 1–2 years following metamorphosis (Caldwell, 1987). This fairly short lifespan can make them particularly susceptible to environmental and habitat changes. Still, there are no studies exploring the factors influencing postmetamorphic demographic rates for this species, partially because there is a lack of information on effective marking methods that allow for individual or cohort identification.

Here, we focus on exploring survival, mark loss, and mark retention rates for recently metamorphosed Boreal Chorus Frogs, predicting that metamorphs may be more prone to losing marks (VIE or toe clips) due to their relatively rapid growth and development rates. Our objectives were: (1) determining the potential short-term (three months) and long-term (one year) survival effects of marking postmetamorphic Boreal Chorus Frogs with visual implant elastomer or toe clipping; (2) exploring factors other than marking that may contribute to variation in postmetamorphic survival probabilities (body size and density) and; (3) evaluating mark retention for both methods and mark migration rates for VIE.

MATERIALS AND METHODS

Experimental design.—We obtained 147 recently metamorphosed Boreal Chorus Frogs reared from tadpoles from June to August 2010 from a captive colony at Colorado State University (CSU). All tadpoles were collected from a mixture of agricultural and rural ponds in Larimer County, Colorado, at elevations ranging from 2,300 m to 2,900 m with random dip net sweeps. Postmetamorphic individuals were held in GladWare containers (4.5 × 9.4 × 13.0 cm, 3 L) in the CSU Aquatic Research Laboratory. Containers held a wetted bottom layer of eco-earth (sterile coconut fiber substrate, Zoo Med Laboratories Inc., San Luis Obispo, CA), a clump of damp moss, and a water dish. The recently metamorphosed frogs were kept in a 12:12 light:dark cycle, a temperature of 19°C, and fed a diet of fruit flies and small crickets 5–6 times per week. Later, their diet was switched to larger crickets given three times per week. Three frogs were assigned randomly to each container because this density has been shown to have no influence on growth and survival of Boreal Chorus Frogs in a previous laboratory experiment (S. M. Amburgey, CSU, unpubl. data).

Containers were randomly assigned to a VIE (Northwest Marine Technology Inc., Shaw Island, WA), toe-clip, or control group, and the container location was randomly assigned to avoid microclimate effects on growth and survival. Three variations of both marking treatments were employed to individually identify frogs within each container. For example, within each VIE treatment container we marked each individual with a single VIE mark but in different locations, either the back left foot, the back right foot, or the front right foot. Similarly, within each toe clip treatment container there were three variations of clips given to individual frogs according to the Martof (1953) system. We marked one individual as ''51'' (denoting two toes clipped on the back right foot), a second individual as ''3250'' (one toe clipped on the front right foot and one toe clipped on the back right foot), and the last individual was marked as ''405'' (one toe clipped on the front left foot and one toe clipped on the back left foot). The last group was frogs that were not marked (control). Photographs and size measurements were used to differentiate individuals within these containers.

Each frog was measured (snout–vent length, SVL) to the nearest mm with dial calipers and photographed at 4–6-week intervals for one year (11 sample occasions). At this time, the number of surviving individuals in each container at the end of the sample occasion was also recorded. Each frog began the experiment with two container mates but this changed over time as some individuals died, reducing the density within some containers and potentially affecting survival probabilities for remaining frogs via reduced competition. Mark retention and migration were recorded bi-monthly for all surviving marked individuals using two independent observers (JS and LB).

Survival probability.—To address our first two objectives, we used known-fate models to estimate survival probabilities, namely, the probability that an individual survives a 4–6-week period, and evaluate the relative influence of our various factors including marking method, individual size, density, and time (Williams et al., 2002). We compiled detection histories for each individual frog and assigned them to one of four attribute groups: visual implant elastomer (VIE, $n = 48$), toe clipped with code 3250 or 405 (TC1, $n = 31$), toe clipped with code 51 (TC2, $n = 17$), and control ($n = 51$). The toe clipped frogs were separated into two attribute groups because we were interested in whether clipping multiple toes on a single foot (TC2) resulted in lower survival compared to clipping a single toe on multiple feet (TC1). Two time-varying individual covariates were also included in the analysis, size and the number of container mates, as these factors may influence survival probabilities regardless of an individual's marked status. All known-fate analyses were conducted using Program MARK (White and Burnham, 1999).

Thirty-four models (Appendix 1) were fit to the data described above to explore factors expected to influence survival probabilities of Boreal Chorus Frogs post metamorphosis. We were most interested in determining whether survival probabilities for marked individuals were lower than those of the control individuals and if this relationship varied over time. Our most general model, S(4trt*t), allowed survival probabilities to vary independently among the four attribute groups (treatments) and over time. Marking effects were formally examined by considering models where survival probabilities: (1) differed among the four attribute groups (denoted ''4trt''); (2) differed among VIE, toe clipped, and control treatments (denoted ''3trt''; all toe clipped individuals have the same probability); (3) differed among marked and control frogs (models denoted ''2trt''; no survival difference among marking treatments); or (4) were the same for all frogs (models denoted ''.'' or lacked a

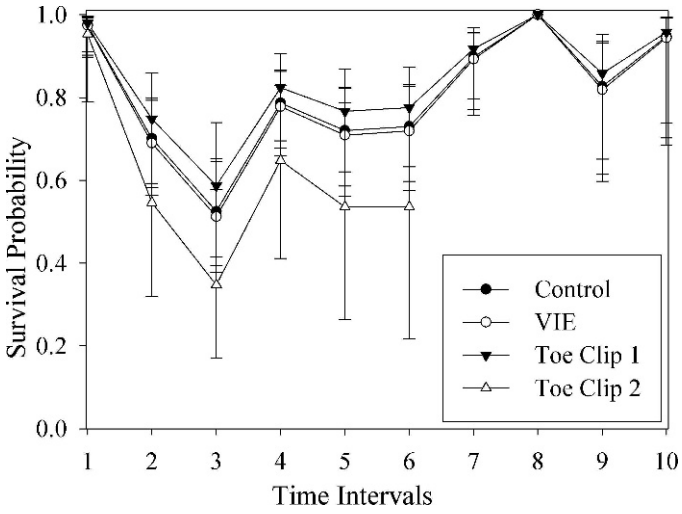

Fig. 1. Model average estimates and corresponding confidence intervals of Boreal Chorus Frog survival probability for each attribute group over a one-year laboratory experiment. Time intervals are 4–6 weeks. Toe Clip 1 denotes frogs with a single toe clipped on two separate feet, Toe Clip 2 denotes frogs with two toes clipped on the same foot, and VIE denotes frogs marked with visual implant elastomer.

treatment designation). We suspected that survival probabilities may vary over time periods within our study, t, with higher mortality during the first few months following metamorphosis and initiation of the treatments (Bailey et al., 2004). Thus, we compared models with no time effect to those where survival probabilities varied independently among groups and occasions (denoted as interaction ''*t'') and to those where time had an additive effect, ''+t''. We also considered models with a linear time trend (T) that were either additive (+T) or interactive (*T) among groups. Finally, we investigated whether variation in survival probabilities was better explained by our individual covariates (body size and container density). We considered models where survival probabilities were an additive or interaction function of size (SVL) or density (number of container mates, ''CM''). We expected survival probabilities to be higher for larger individuals and higher for individuals with fewer container mates.

After completing the above analysis, we fit two *post-hoc* models that suggested that individuals with multiple toes clipped on the same foot had different survival probability than all other treatments, denoted S(TC2,others+t) and S(TC2,others*t). These models were added after it was observed that all the frogs with two toes clipped on the same foot had died during the first four months of the experiment (Fig. 1).

Mark retention and migration.—To address our last objective, we simply counted the number of marks that were retained in the VIE and toe clip treatments and the number of marks that migrated in the VIE treatment three months into the experiment (short-term) and again one year into the experiment (long-term). Percentage of mark retention and mark migration was calculated separately for individuals marked with VIE or toe clips. Toe clip migration is not possible, but mark loss was considered regeneration of the clipped toe. VIE mark migration was observed as the original mark breaking into small specks of elastomer and drifting freely throughout the frog's body, usually concentrating in the abdominal area. Mark loss was recorded when there appeared to be no remaining trace of elastomer in any part of the frog's body.

RESULTS

Survival probabilities.—Out of the 147 individuals alive at the beginning of our study (control $n = 51$, VIE $n = 48$, TC1 $n = 31$, and TC2 $n = 17$), 21 individuals survived the duration of the experiment (control $n = 7$, VIE $n = 5$, TC1 $n = 7$, and TC2 $n = 0$). Model selection results supported six models ($w_i \geq 0.01$) including our two *post-hoc* models (Table 1). Our most supported model, S(4trt+t) $w_i = 0.49$, suggested that survival probabilities differed between the four treatment groups with an additive time effect. Under this model, we found that relative to the control group, individuals that had a single toe clipped on each foot had slightly higher survival probabilities (effect size on the logit scale: $\hat{\beta}_{TC1} = 0.51$, 95% CI: − 0.07, 1.09; the odds ratio (OR) = $e^{\hat{\beta}_{TC1}} = 1.67$), VIE marked individuals had nearly equivalent survival probabilities to the control individuals ($\hat{\beta}_{VIE} = -0.11$, 95% CI: − 0.62, 0.40; (OR) = 0.90), and individuals with two toes clipped on the same foot had lower survival probabilities ($\hat{\beta}_{TC2} = -0.77$, 95% CI: − 1.54, 0.09; (OR) = 0.46). Our model with the most support was about 1.5 times as likely (evidence ratio = 1.44) as the second most supported model, S(TC2,others+t) $w_i = 0.34$, but both models suggested that individuals with two toes clipped on the same foot had a lower survival probability than all other individuals with additive time variation. The third model, which garnered little weight, S(t) $w_i = 0.07$, was the only supported model to suggest that survival probabilities did not differ among treatment groups. All supported models suggested that survival probability differed over time, with a decline in survival probability during the first two months, then a gradual increase in survival probability over the remainder of the study (Fig. 1). Using model averaging (Anderson and Burnham, 2002), we estimated the probability that an unmarked individual would survive its first year post metamorphosis was 0.129 (SE = 0.04). Similarly, individuals marked with VIE or a single toe clip per foot had annual survival probabilities of 0.118 (SE = 0.04) and 0.196 (SE = 0.08), respectively. Frogs with two toes clipped on one foot all died approximately four months after marking ($n = 17$; Fig. 1). Interestingly, among VIE marked frogs, only frogs injected in the front foot were surviving at the end of the year ($n = 5$). This may indicate that these individuals have a higher survival rate than frogs injected in their back feet, especially considering that there were twice as many individuals marked in a back foot than a front foot at the beginning of the study ($n = 32$ individuals injected in a back foot, $n = 16$ injected in the front foot).

Mark retention and migration.—Three of 48 individuals lost their VIE marks completely in the first three months, but no other mark loss was observed for the remainder of the study. Two other individuals experienced mark migration during the first three months when the original mark had broken up into small specks of elastomer drifting freely throughout the frog's body and concentrating in the abdominal area. Mark migration was impossible for toe clipped individuals and we observed 100% retention of toe clips throughout the study.

DISCUSSION

Numerous studies have stressed the importance of the postmetamorphic life stages to better understand the complex dynamics of amphibian populations (Biek et al.,

Table 1. Model Selection Results for Known-fate Survival Models of Boreal Chorus Frogs. Model weight given for both the original model set, *org* w_i, and when two *ad-hoc* models were added, *full* w_i. The number of parameters (K) and relative model fit (deviance) are given for each supported model. Variable definitions: 4trt = all four attribute groups have different survival; TC2,others = frogs with two toes clipped on the same foot have different survival probabilities than all other individuals; . = all four attribute groups have the same survival probability; 2trt = all treated individuals have a different survival probability than control individuals; 3trt = VIE attribute group, both toe clip attribute groups, and the control attribute group have different survival probabilities; +t = additive time effect; *t = interactive time effect.

Model	AIC_c	ΔAIC_c	*org* w_i	*full* w_i	K	Deviance
S(4trt+t)	604.74	0.00	0.81	0.49	13	578.21
S(TC2,others+t)†	605.45	0.71	—	0.34	11	583.07
S(t)	608.61	3.87	0.12	0.07	10	588.30
S(TC2,others*t)†	609.03	4.29	—	0.06	16	576.24
S(2trt+t)	610.65	5.91	0.04	0.03	11	588.27
S(3trt+t)	611.69	6.95	0.03	0.02	12	587.24

† *Post-hoc* model

2002; Conroy and Brook, 2003; Di Minin and Griffiths, 2011). Estimates of demographic parameters are still lacking for these life history stages in most amphibian species, especially for juveniles, which are often difficult to mark and recapture. We found that survival probabilities of postmetamorphic Boreal Chorus Frogs differed depending on marking technique, with lower survival rates exhibited by individuals that had more than one toe clipped on the same foot. Although we predicted a difference in survival among treatments, we also saw that survival of all individuals varied throughout the year. Survival probabilities declined during the first 3–4 months post metamorphosis (Fig. 1), but then increased in the remaining eight months for all treatments except TC2. Survival probabilities after the first few months were particularly low compared to other time periods, but we observed nothing which would indicate disease as the cause of lowered survival probabilities during this time. Moreover, there was no indication that the variation in survival was due to individual body size or densities within the containers as models with these covariates were not well supported. Still, we observed remarkable temporal variation in survival probabilities throughout the year, from values ≤0.60 for all treatments in some periods to nearly all individuals surviving other periods. These results may not be surprising given the relative vulnerability of postmetamorphic life stages in many amphibian species (Biek et al., 2002; Conroy and Brook, 2003), but it was interesting that we observed such high variability within the stable conditions of our laboratory experiment.

Although the pattern of fluctuation of survival probabilities over time was similar for all treatment groups, by using our model averaged estimates we found that annual survival rates of metamorphs marked with VIE or a single toe clipped on two separate feet were comparable to control individuals (approximately 10–20%). To our knowledge, these are the first estimates of metamorph survival probabilities ever reported for *Pseudacris* and are similar to derived estimates used in sensitivity analysis for other anuran species (e.g., Biek et al., 2002, who acknowledge that no quantitative estimates exist for their target species). No frogs marked with two toes clipped on the same foot survived the entire year of the study. Previous research involving adult anurans indicated that the total number of toe clips is important (Waddle et al., 2008), but our study shows that the placement of clips may also play a principal role in individual survival probability and we encourage others to investigate the influence of certain marking combinations in future demographic studies.

Our study provides clear direction for investigators interested in studying juvenile life-history stages in natural populations. We found that individuals can be marked by clipping a single toe on two feet without any mark loss or negative survival effects. Individuals marked with VIE also showed no survival effects, but we found low levels of mark loss (n = 3, 6%) and mark migration (n = 2, 4%) that occurred soon after injection and then did not change further during the year. These observations correspond with other VIE studies in adult frogs (Nauwelaerts et al., 2000; Moosman and Moosman, 2006; Hoffman et al., 2008), suggesting that some low-level mark loss should be expected with VIE marking.

In most investigations, only minimal toe clipping of postmetamorphic (particularly recently metamorphosed) amphibians is necessary to address the majority of demographic questions. These questions are likely to focus on the spatial and temporal variation of postmetamorphic vital rates, which can be evaluated using a unique cohort mark to identify the year and location of metamorphosis. If an individual is captured in later years as an adult it may be given a second, individually unique mark with another technique, such as pit tagging (e.g., Fellers and Kleeman, 2007) or using photo identification (e.g., Church et al., 2007) that would be retained throughout its lifetime. Researchers who are interested in factors that may influence juvenile vital rates such as individual size or time of metamorphosis could apply different cohort marks to these groups within the same year and location (for example, small vs. large individuals or individuals that metamorphosed relatively early or late in during a particular season).

However, toe clipping may become impractical for studies involving a large number of groups or locations, or those continuing for many years, as the number of unique cohort marks with few toes clipped is limited. In these cases, considering VIE as an alternative or additional marking method may be beneficial, despite the method's low rates of loss and migration. If the same strategies for cohort marking are employed using VIE, mark migration is unlikely to be a problem because the individual can still be matched to the correct marked cohort, though mark loss could still bias vital rate estimates. Several recent studies support using a combined marking method of VIE and toe clips (VIE-C, Hoffmann et al., 2008; Campbell et al., 2009). Combining these two techniques expands the number of cohort marks

available (Hoffman et al., 2008) and provides a way of estimating and adjusting for mark loss (Williams et al., 2002). By taking these results into consideration, researchers and managers can develop appropriate marking methods for their biological questions of interest.

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APPENDIX 1. Name and description of models (hypotheses) used for testing the effects of treatment groups (trt), time variation, density, and size on Boreal Chorus Frog survival probabilities (S). VIE, TC1, TC2, Control denotes a model where all four attribute groups had different survival probabilities; VIE, TC1 = TC2, Control denotes a model where the VIE, toe clip (of any kind), and control attribute groups had different survival probabilities; VIE = TC1 = TC2, Control suggests all marked treatment attribute groups had similar survival probabilities but they were different than the control group; VIE = TC1 = TC2 = Control denotes all attribute groups had the same survival probability; TC2, VIE = TC1 = Control denotes the toe clip group with two toes clipped on the same foot had a different survival probability than all other individuals.

Model	Hypothesis description
S(4trt+t)	VIE, TC1, TC2, Control with an additive time effect
S(4trt*t)	VIE, TC1, TC2, Control with an interactive time effect
S(4trt+T)	VIE, TC1, TC2, Control with an additive, linear time trend
S(4trt*T)	VIE, TC1, TC2, Control with an interactive linear time trend
S(4trt)	VIE, TC1, TC2, Control
S(4trt+SVL)	VIE, TC1, TC2, Control with an additive size effect
S(4trt*SVL)	VIE, TC1, TC2, Control with an interactive size effect
S(4trt+CM)	VIE, TC1, TC2, Control with an additive density effect
S(4trt*CM)	VIE, TC1, TC2, Control with an interactive density effect
S(3trt+t)	TC1 = TC2, VIE, Control with an additive time effect
S(3trt*t)	TC1 = TC2, VIE, Control with an interactive time effect
S(3trt+T)	TC1 = TC2, VIE, Control with an additive = linear time trend
S(3trt*T)	TC1 = TC2, VIE, Control with an interactive linear time trend
S(3trt)	TC1 = TC2, VIE, Control
S(3trt+SVL)	TC1 = TC2, VIE, Control with an additive size effect
S(3trt*SVL)	TC1 = TC2, VIE, Control with an interactive size effect
S(3trt+CM)	TC1 = TC2, VIE, Control with an additive density effect
S(3trt*CM)	TC1 = TC2, VIE, Control with an interactive density effect
S(2trt+t)	VIE = TC1 = TC2, Control with an additive time effect
S(2trt*t)	VIE = TC1 = TC2, Control with an interactive time effect
S(2trt+T)	VIE = TC1 = TC2, Control with an additive = linear time trend
S(2trt*T)	VIE = TC1 = TC2, Control with an interactive linear time trend
S(2trt)	VIE = TC1 = TC2, Control
S(2trt+SVL)	VIE = TC1 = TC2, Control with an additive size effect
S(2trt*SVL)	VIE = TC1 = TC2, Control with an interactive size effect
S(2trt+CM)	VIE = TC1 = TC2, Control with an additive density effect
S(2trt*CM)	VIE = TC1 = TC2, Control with an interactive density effect
S(t)	VIE = TC1 = TC2 = Control with an interactive time effect
S(T)	VIE = TC1 = TC2 = Control with an additive = linear time trend
S(.)	VIE = TC1 = TC2 = Control
S(SVL)	VIE = TC1 = TC2 = Control with an additive size effect
S(CM)	VIE = TC1 = TC2 = Control with an additive density effect
S(TC2 = others+t)†	TC2, VIE = TC1 = Control with an additive time effect
S(TC2 = others*t)†	TC2, VIE = TC1 = Control with an interactive time effect

† *Post-hoc* model