SHORT COMMUNICATION

Effect of weather conditions on cohort splitting in a wolf spider species

Zoltán Rádai[1*], **Balázs Kiss**[2] and **Ferenc Samu**[2]: [1]MTA-DE Lendület Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary; E-mail: zradai.sci@gmail.com [2]Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, Budapest, Hungary

Abstract. Cohort splitting has been described as differences in time until maturation and / or life span in the same age group. Cohort splitting generally occurs when individuals of a cohort originating from the same season experience different environmental conditions, such as in early and late progenies. However, in the wolf spider *Pardosa agrestis* (Westring, 1861) spiderlings of the same clutch may follow either slow or rapid development, leading to a second adult peak within a year comprised of the rapidly developing individuals. We hypothesized that weather conditions experienced by the spiderlings in their early ontogeny may contribute to a life history decision between slow and rapid development. To test this hypothesis, we have used long term collection data and non-parametric habitat modeling. We found that highest abundance of the rapidly developing phenotype was correlated with a narrow range of early weather conditions. This result is in accordance with our early choice hypothesis, although the possibility remains that differential survival of the developmental morphs also contributes to the observed pattern.

Keywords: Lycosidae, habitat modeling, long term sampling, development, ontogeny

Cohort splitting can be defined as a life history scenario in which individuals within a cohort exhibit variation in developmental rates, maturation time and / or life span, leading to a divergence of individual ontogenies within an age group (Danks 1992; Watts & Thompson 2012; Crowley & Hopper 2015). This phenomenon is well described in several arthropod groups (Sunderland et al. 1976; David et al. 1993; Moreira & Peckarsky 1994; Townsend & Pritchard 1998; David et al. 1999; Bonte & Maelfait 2001; Johansson et al. 2001; Gonçalves et al. 2005; Kozáčeková et al. 2009), as well as in some vertebrates (Newman 1989, 1992; Post et al. 1997; Callihan et al. 2008).

Different factors may play a role in orchestrating cohort splitting, such as genetic polymorphism, maternal effects and environmental cues (reviewed in Crowley & Hopper 2015). Cases of environmentally induced differences in developmental trajectories are well described in animals, for example in relation to population density (Post et al. 1997), prey availability (Pickup & Thompson 1990), ambient temperature (Callihan et al. 2008) or photoperiod (Kozáčeková et al. 2009). Such changes in developmental trajectories due to environmental factors are often regarded as bet-hedging strategies in unpredictable environments (Stearns & Crandall 1981; Tuljapurkar 1994; Watts & Thompson 2012), and can have considerable impact on the fitness of the individuals (Hopper 1999).

An interesting case of cohort splitting was described in populations of the wolf spider *Pardosa agrestis* (Westring, 1861), an epigeic spider species, dominant in agricultural habitats of Central Europe (Samu & Szinetár 2002). Unlike the typical univoltine *Pardosa* life cycles in the temperate regions—where generally one sexually mature cohort exists in each year (see Schaefer 1977)—this semelparous species exhibits a phenology with two adult peaks, and hence two reproductive periods in a year (Samu et al. 1998). As Kiss and Samu (2002, 2005) have shown, this phenological pattern arises from developmental asynchrony in the early summer progeny. Some of the spiderlings, hatching from the first adult generation, between May and June, are only able to reach maturity in the next spring or summer, after overwintering. Others, even from the same brood, are capable of reaching adulthood and reproduce in about three months, thus comprise a second generation within a year (Fig. 1).

The background of this case of cohort splitting is largely unknown, although previous studies suggested that photoperiod and ambient temperature might be key factors, as spiderlings experiencing long day-length and high (but not stressful) temperatures matured sooner and in higher proportions compared to spiderlings reared in short day-length and lower temperatures (Kiss & Samu 2002; Rádai, unpublished results). In artificial rearing experiments, the ratio of slowly and rapidly developing spiderlings varies among clutches (i.e., among mothers) which might indicate genetic involvement in the rapid development (Kiss 2003; Rádai et al.; unpublished data). Still, the strong influence of ambient conditions suggests that cohort splitting may be the result of a decision on the part of the offspring, in an early time window of their ontogeny.

In this study we propose an early choice hypothesis, stating that weather conditions experienced by the early summer progeny of *P. agrestis* contribute to a decision between slow and rapid developmental life histories. Based on the results presented by Kiss and Samu (2002) and Kiss (2003), in an early choice scenario we predict to see that under a narrow range of favourable early weather conditions more spiderlings will choose rapid development. Hence, in years when early weather conditions fall in this narrow range, we would expect to see higher abundances of second generation adults during late summer in natural *P. agrestis* populations. To test this hypothesis, we have used long term collection data from the natural habitats of this spider species in Hungary (Samu 1999), and long term weather data provided by the CarpatClim project (Szalai et al. 2012).

Our working data table consisted of 535 samples (with a total of 5284 collected adult *P. agrestis* specimens), recorded between 1993 and 2002 in the months from August to November, from the vicinity of 13 settlements across Hungary. For each sample we defined sampling success as the number of adult spiders collected with a given sampling method, at the sampling site and date. Sampling method was either suction sampling or using pitfall traps. Because suction sampling and pitfall traps might differ in how they relate sampling success to density and activity of the animals, our records of sampling successes reflected a combination of both abundance and activity during sampling. In all cases, sampling effort was specified as the number of pitfall traps used, or number of sampling transects of identical lengths (10 meters) for suction sampling. For early weather
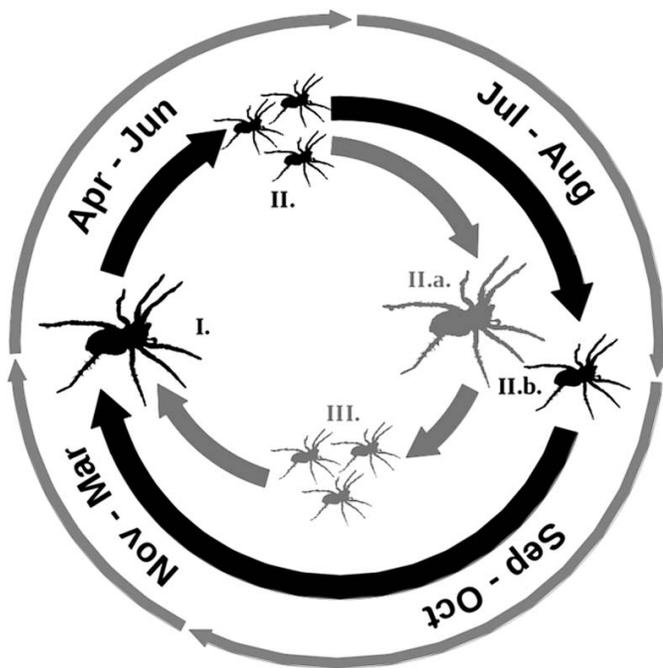
Figure 1.—Phenology of *P. agrestis*; the first adult generation matures between the end of March and April (I.), after which the first wave of progeny hatches in May and June (II.). Some of the spiderlings follow slow development (II.b.) reaching maturity only in the next year, while others develop rapidly, mature and reproduce between August and September (II.a.), giving rise to a new cohort of progeny (III.).

conditions, principal components (PCs) were calculated for May. We also calculated PCs for the given month of sampling. In the PC analyses, we used six weather parameters for each month, measured at the settlement of the sampling location. The spatial detail of available weather data was 10×10 km, therefore we had unique weather data for settlements being at least 10 km apart from one another. The weather parameters were minimum, maximum and mean monthly temperature (Celsius), amount of precipitation (mm), monthly mean of relative humidity and total of sunshine hours in the given month. From the calculated PCA axes, we have used only those with eigenvalues of 1 or higher (Kaiser criterion: Kaiser 1960), which yielded two PCs for May (hereafter, PC1 and PC2 of May) and two for the sampling dates (hereafter PC1 and PC2 of sampling date). The proportions of variance represented by PC1 and PC2 of May were ca. 74 and 17%, respectively. Also, the proportions of variance represented by PC1 and PC2 of sampling-date were ca. 60 and 20%, respectively. PC1 of both May and the sampling date was strongly correlated with all six weather parameters, and PC2 of both May and the sampling date were at least moderately correlated with all weather parameters (see supplementary material for details, online http://dx.doi.org/10.1636/JoA-S-17-008R2.s1).

To test, how the calculated PCs for May and for the sampling dates are related to the sampling success of second generation adults in the months between August and November, we have applied non-parametric habitat modeling using HyperNiche v2.30 (McCune & Mefford 2009). In the models, we defined sampling success as response variable, while predictor variables were the calculated principal components for the weather of May and sampling date weather. As additional predictors we also used habitat type (categorical, with levels: arable field, wet meadow, alkaline grassland, rock grassland, disturbed grassy habitat), sampling method (categorical, with levels: pitfall traps or suction sampling) and sampling effort.

Models were acquired by running three model-searching sessions of Local Linear Estimator, using conservative, medium and aggressive over-fitting settings, respectively (3% allowable missing estimates in each). Each session yielded a high number of models, from which the one with the highest cross-validated R^2 value was selected as the best fit, so finally we had one model from each session (i.e., three models in total). To test whether the fitted models are better than could be obtained by chance alone, we have used randomization tests (integrated in HyperNiche) with 100 runs, comparing each model to 100 models with randomly generated predictor values.

In all three best fit models, sampling method and PC1 of May were retained as predictor variables, indicating that out of the tested variables, these consistently explained the variance in sampling success best. Additionally, in the models using medium and aggressive over-fitting settings, PC1 of the sampling date was also retained. All three models explained sampling success significantly better than did randomized predictor values ($P = 0.01$ in case of all models). Based on the models, highest second generation adult abundances were related to a narrow range of early weather conditions in May (see Fig. 2). Similarly, in the models using medium and aggressive over-fitting, a narrow range of sampling date weather conditions was also apparent, at which sampling success peaked (Fig. 2). Regarding the sampling methods, on average pitfall traps collected more spiders per sample compared to suction sampling; estimated sampling success of pitfall traps and suction sampling were 12.41 ± 22.97 and 1.98 ± 1.58 (mean ± standard deviation), respectively.

The selected models' consistent retainment of the PC representing weather conditions in May indicates that early conditions strongly influence the abundance of the second adult generation. The relatively narrow range in the values of May PC1 corresponding to high second generation abundance can be regarded as an optimal set of weather conditions, which enable or contribute to the appearance and high abundance of rapidly developing individuals in the populations.

Although our results support that weather conditions during early larval stages contribute significantly to the abundance of rapidly developing spiders, the mechanism in the background remains unclear. Environmental factors may affect postembryonic development directly, for example through providing cues based on which life history decisions can be made (reviewed in Danks 1994). However, they can act indirectly as well, for example due to their effects on prey availability (Hayashi 1988) or metabolism (Gillooly et al. 2001). In years of drought, low prey abundance might limit the opportunities of the spiders because limited prey availability possibly cannot provide sufficient quantity and / or quality of resources for rapid growth. On the other hand, low temperatures during the first larval stages could lengthen developmental time either by reducing the efficiency of different metabolic processes (Brown et al. 2004; Irlich et al. 2009), or simply by decreasing locomotory activity of the animals (Ford 1978), leading to reduced hunting virtue.

Furthermore, differential survival of spiderlings of alternate developmental trajectories could also contribute to the correlation between late summer adult abundance and weather conditions in May. More precisely, it might be possible that the ratio of slowly and rapidly developing spiders (not assessed in this study) is not as strongly related to environmental cues, e.g., due to genetic polymorphism, and the abundance of late summer adults is affected also by their survival throughout the first larval stages. For instance, spiderlings engaging in rapid development have probably higher demand for energy and nutrients, which, if not met, could lead to increased mortality among rapidly developing spiderlings when food is scarce. Therefore, we cannot rule out that late summer abundance of adults, at least in part, is shaped by the differential survival of the two developmental phenotypes during their early ontogeny. However, considering the results of past rearing studies, in which ambient conditions were shown to increase moulting frequency and probability of moulting to adulthood (Kiss & Samu 2002; Kiss 2003), it seems
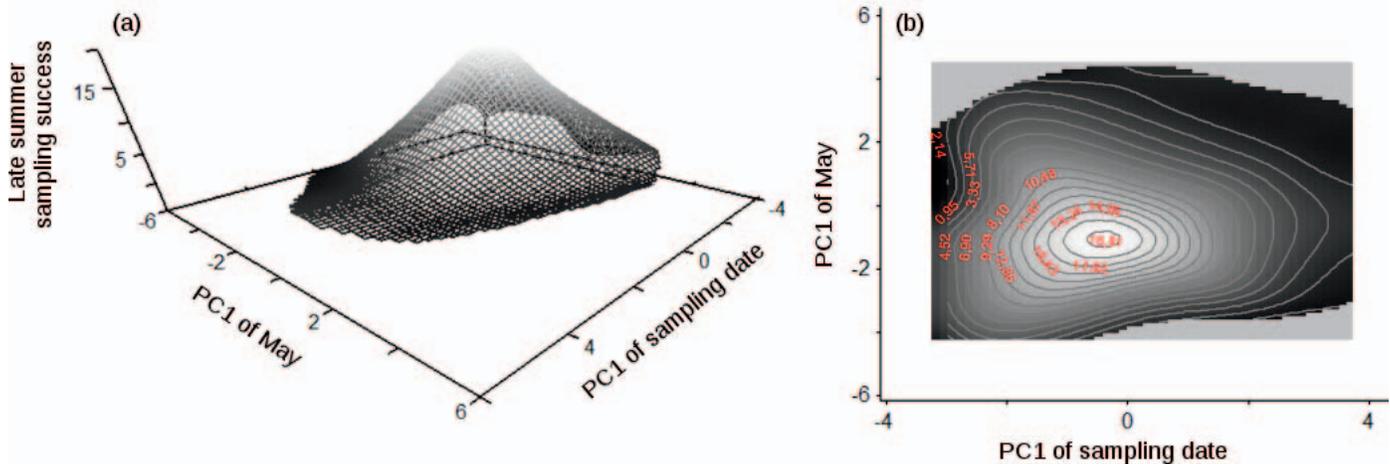
Figure 2.—Sampling success of late summer adults in relation to weather conditions in May and during sampling, visualized on 3D projection plot (a) and contour plot (b). Structural lines on (a) and contour regions on (b) represent the number of adult *P. agrestis* individuals: darker lines / regions correspond to low, while bright lines / regions correspond to higher numbers. On the contour plot (b) gray lines delimit the segments of the response surface of late summer sampling success, and red numbers show the predicted sampling success (i.e., number of adult spiders), in relation to weather conditions in May (PC1 of May) and during sampling (PC1 of sampling date).

likely that weather conditions experienced by the spiderlings in their early ontogeny have a consistent and profound effect on their development.

The result that weather conditions during the month of sampling show similar effect on the abundance of adults suggests that weather also influences sampling success itself, which is not very surprising, since environmental conditions are known to contribute to the activity, and thus the sampling success of epigeic arthropods (e.g., Honěk 1988; Kiss & Samu 2000). Under favourable weather conditions in late summer adult spiders might show increased activity due to increased propensity to forage, or to look for potential mates, leading to an increase in their sampling success. On the other hand, severely adverse conditions might not only decrease their activity, but could also increase mortality, leading to significant reduction in population size, and consequently to low sampling success. We note that because the two sampling methods might represent activity and abundance with different weights, by including both types of data, and also sampling method as a factor in our models, we could base our interpretation of the results on an intermediate estimate of activity and abundance.

In Hungarian *P. agrestis* populations, cohort splitting is a persistent phenomenon (Samu et al. 2011), but its degree is dependent on both the early summer and late summer weather conditions of the given year. This versatile life history strategy of *P. agrestis*, that is unique among congeneric wolf spiders, may represent a special adaptation to climatic conditions in Central Europe, making this species able to benefit from variably occurring favourable periods. Cohort splitting may have preadapted *P. agrestis* to highly changeable agricultural environments, and could be a reason why it has become a successful agrobiont species that attains high abundances in arable habitats (Kiss & Samu 2005).

In conclusion, our results are in accordance with the prediction of our early choice hypothesis, although in this study we cannot rule out that differential survival of the two developmental forms might also contribute to the observed pattern. The exact mechanism by which early weather affects the life histories of *P. agrestis* and evokes cohort splitting remains to be studied. Also, it is likely that not only early weather conditions contribute to this case of cohort splitting, so within- and among brood variation in life histories unrelated to weather conditions should also be considered in future studies. Arguably, retrospective approaches using long term data on

population ecology and high-throughput modeling methods offer valuable insights on population dynamics, and therefore could be valuable tools when studying cohort splitting. The present example of cohort splitting still holds relevant and important questions regarding its background, function and consequences on the spiders' life histories. In the future, common garden tests and linear or multigenerational heritability studies might make it possible to assess the nature and origin of this case of cohort splitting.

LITERATURE CITED

Bonte, D. & J. P. Maelfait. 2001. Life history, habitat use and dispersal of a dune wolf spider (*Pardosa monticola* [Clerck, 1757] Lycosidae, Araneae) in the Flemish coastal dunes (Belgium). Belgian Journal of Zoology 131:145–157.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage & G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Callihan, J.L., L.T. Takata, R.J. Woodland & D.H. Secor. 2008. Cohort splitting in bluefish, *Pomatomus saltatrix*, in the US mid-Atlantic Bight. Fisheries Oceanography 17:191–205.

Crowley, P.H. & K.R. Hopper. 2015. Mechanisms for adaptive cohort splitting. Ecological Modelling 308:1–13.

Danks, H.V. 1992. Long life cycles in insects. Canadian Entomologist 124:167–187.

Danks, H.V. 1994. Diversity and integration of life-cycle controls in insects. Pp. 5–40. *In* Insect life-cycle polymorphism (H.V. Danks (ed.)). Springer Science+Business Media, Dordrecht.

David, J.F., M.L. Celerier & J.J. Geoffroy. 1999. Periods of dormancy and cohort-splitting in the millipede *Polydesmus angustus* (Diplopoda: Polydesmidae). European Journal of Entomology 96:111–116.

David, J.F., T. Couret & M.L. Celerier. 1993. The life cycle of the millipede *Polydesmus angustus*: another case of cohort-splitting. European Journal of Soil Biology 29:117–125.

Ford, M.J. 1978. Locomotory activity and the predation strategy of the of the wolf-spider *Pardosa amentata* (Clerck) (Lycosidae). Animal Behaviour 26:31–35.

Gillooly, J.F., J.H. Brown, G.B. West, V.M. Savage & E.L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gonçalves, S. C., M.A. Pardal, P.G. Cardoso, S.M. Ferreira & J.C. Marques. 2005. Biology, population dynamics and secondary production of *Tylos europaeus* (Isopoda, Tylidae) on the western coast of Portugal. Marine Biology 147:631–641.

Hayashi, F. 1988. Life history variation in a dobsonfly, *Protohermes grandis* (Megaloptera: Corydalidae): effects of prey availability and temperature. Freshwater Biology 19:205–216.

Honěk, A. 1988. The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera), and Lycosidae (Araneae) in cereal fields. Pedobiologia 32:233–242.

Hopper, K.R. 1999. Risk-spreading and bet-hedging in insect population biology. Annual Review of Entomology 44:535–560.

Irlich, U.M., J.S. Terblanche, T.M. Blackburn & S.L. Chown. 2009. Insect rate temperature relationships: environmental variation and the metabolic theory of ecology. American Naturalist 174:819–835.

Johansson, F., R. Stoks, L. Rowe & M. De Block. 2001. Life history plasticity in a damselfly: Effects of combined time and biotic constraints. Ecology 82:1857–1869.

Kaiser, H.F. 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20:141–151.

Kiss, B. 2003. Autecology of the wolf spider *Pardosa agrestis* (Westring, 1861). PhD dissertation, University of Veszprém, Hungary.

Kiss, B. & F. Samu. 2000. Evaluation of population densities of the common wolf spider *Pardosa agrestis* (Araneae : Lycosidae) in Hungarian alfalfa fields using mark-recapture. European Journal of Entomology 97:191–195.

Kiss, B. & F. Samu. 2002. Comparison of autumn and winter development of two wolf spider species (*Pardosa*, Lycosidae, Araneae) having different life history patterns. Journal of Arachnology 30:409–415.

Kiss, B. & F. Samu. 2005. Life history adaptation to changeable agricultural habitats: Developmental plasticity leads to cohort splitting in an agrobiont wolf spider. Environmental Entomology 34:619–626.

Kozáčeková, Z., J.M.T. de Figueroa, M.J. López-Rodríguez, P. Beracko & T. Derka. 2009. Life history of a population of *Protonemura intricata* (Ris, 1902) (Insecta, Plecoptera) in a constant temperature stream in Central Europe. International Review of Hydrobiology 94:57–66.

McCune, B. & M.J. Mefford. 2009. HyperNiche. Non–parametric multiplicative habitat modeling. Version 2.30. MjM Software, Gleneden Beach, OR, USA.

Moreira, G.R.P. & B.L. Peckarsky. 1994. Multiple developmental pathways of *Agnetina capitata* (Plecoptera: Perlidae) in a temperate forest stream. Journal of North American Benthological Society 13:19–29.

Newman, R.A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology 70:1775–1787.

Newman, R.A. 1992. Adaptive plasticity in amphibian metamorphosis. Bioscience 42:671–678.

Pickup, J. & D.J. Thompson. 1990. The effects of temperature and prey density on the development rates and growth of damselfly larvae (Odonata: Zygoptera). Ecological Entomology 15:187–200.

Post, J.R., M.R.S. Johannes & D.J. McQueen. 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Canadian Journal of Fisheries and Aquatic Sciences 54:867–875.

Samu, F. 1999. A general data model for databases in experimental animal ecology. Acta Zoologica Academiae Scientiarum Hungaricae 45:273–290.

Samu, F. & C. Szinetár. 2002. On the nature of agrobiont spiders. Journal of Arachnology 30:389–402.

Samu, F., J. Németh, F. Tóth, É. Szita, B. Kiss & C. Szinetár. 1998. Are two cohorts responsible for bimodal life history pattern in the wolf spider *Pardosa agrestis* in Hungary? Pp. 215–221. *In* Proceedings 17th European Colloquium of Arachnology, (P.A. Selden (ed.)). Edinburgh.

Samu, F., C. Szinetár, É. Szita, K. Fetykó & D. Neidert. 2011. Regional variation in agrobiont composition and agrobiont life history of spiders (Araneae) within Hungary. Arachnologische Mitteilungen 40:105–109.

Schaefer, M. 1977. Winter ecology of spiders (Araneida). Zeitschrift Fur Angewandte Entomologie-Journal of Applied Entomology 83:113–134.

Stearns, S.C. & R.E. Crandall. 1981. Bet-hedging and persistence as adaptations of colonizers. Pp. 371–383. *In* Evolution Today (G.G.E. Scudder & J.L. Reveal (eds.)). Hunt Institute for Biological Documentation, Carnegie-Mellon University, Pittsburg.

Sunderland, K.D., M. Hassall & S.L. Sutton. 1976. Population dynamics of *Philoscia muscorum* (Crustacea, Oniscoidea) in a dune grassland ecosystem. Journal of Animal Ecology 45:487–506.

Szalai, S., T. Antofie, P. Barbosa, Z. Bihari, M. Lakatos, J. Spinoni et al.2012. The CARPATCLIM project: Creation of a gridded climate atlas of the Carpathian regions for 1961–2010 and its use in the European Drought Observatory of JRC. ECAC2012, Lodz.

Townsend, G.D. & G. Pritchard. 1998. Larval growth and development of the stonefly *Pteronarcys californica* (Insecta: Plecoptera) in the Crow's Nest River, Alberta. Canadian Journal of Zoology 76:2274–2280

Tuljapurkar, S. 1994. Stochastic demography and life histories. Pp. 254–262. *In* Frontiers in Mathematical Biology (S.A. Levin (ed.)). Springer, Berlin Heidelberg.

Watts, P.C. & D.J. Thompson. 2012. Developmental plasticity as a cohesive evolutionary process between sympatric alternate-year insect cohorts. Heredity 108:236–241.