# Synchronous and Non-Synchronous Semelparity in Sibling Species of Pulmonates

Authors: Nyumura, Nobuhiro, and Asami, Takahiro

Source: Zoological Science, 32(4) : 372-377

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zs150020

ZOOLOGICAL SCIENCE **32**: 372–377 (2015)

# Synchronous and Non-Synchronous Semelparity in Sibling Species of Pulmonates

**Nobuhiro Nyumura and Takahiro Asami***

*Department of Biology, Shinshu University, Matsumoto 390-8621, Japan*

**Diverse life histories have been documented in terrestrial pulmonates, which inhabit different regions in climate. Life history traits are often phenotypically plastic and vary depending on the environment. Thus, surveys using designs that control for the confounding effects of environment are needed to evaluate the evolutionary differences between populations of closely related species in the wild. We examined the life histories of sibling species of terrestrial pulmonate within two regions of similar climates. *Bradybaena pellucida* (BP) is endemic to Japanese islands, and has recently been expanding its distribution northeastward, whereas *B. similaris* (BS) has been introduced by humans into temperate and tropical regions worldwide. We found that these species exhibit discrete differences in population dynamics and life cycle, despite their close relatedness. The annual life cycle of BP is synchronized among individuals in a population. Thus, BP is univoltine with discontinuous generation. In contrast, BS individuals do not synchronize their growth or reproduction, and thus exhibit overlapping generations. Our results indicate that synchronized and non-synchronized population dynamics diverge relatively rapidly in semelparous pulmonates. This type of difference has not been documented in pulmonate life history, and may have been overlooked because only a few studies have explicitly compared life cycles of closely related species within the same climate. Our results provide a basis for further studies of life history evolution in pulmonates.**

**Key words:** life cycle, life history, population dynamics, land snail, *Bradybaena*, Gastropoda

## INTRODUCTION

The life histories of animals and plants can be categorized as iteroparous or semelparous; iteroparity refers to repeated reproduction over separate periods in individual lifetime, whereas semelparity is characterized by death after reproduction in a single period (Roff, 1992; Young, 2010). This way of contrasting different life histories provides useful insights into the evolution of reproductive strategies. Among diverse organisms, however, distinctions between these categories may not necessarily be generally applicable, and remain controversial (Kirkendall and Stenseth, 1985; Hughes and Simons, 2014).

In land gastropods including snails and slugs, Heller (2001) reviewed literature of 20 iteroparous and 15 semelparous genera. Since then, probable iteroparity in the genus *Helicodonta* (Maltz, 2003) and semelparity in *Pupilla* (Pokryszko, 2001) and *Trochulus* (Kuznik-Kowalska et al., 2013a) have been reported. Populations of *Xerolenta obvia* vary from iteroparity to semelparity, perhaps depending on environment (Lazaridou and Chatziioannou, 2005). Even among terrestrial pulmonates, wide ranges of variation have been documented in life span and cycle and other reproductive traits across diverse climatic ranges (Heller, 1990, 2001; Maltz, 2003; Kramarenko, 2013).

To elucidate the processes and mechanisms of ecology and evolution responsible for the diversity of life history, the intra- and interspecific variabilities of target phenotypes need to be understood. Only few studies have, however, examined differences in traits of life history between closely related gastropods. It is difficult to evaluate the effect of environmental differences on a life history phenotype when comparing geographically distant populations in the wild, especially when previous reports in the literature are considered. As an alternative, explicit comparisons in sympatry or climatically similar regions could instead allow the examination of evolutionary differences by minimizing confounding effects of phenotypic plasticity. In the present study, therefore, we focused on a comparison of life history among populations of sibling species in the pulmonate snail genus *Bradybaena* within two regions.

*Bradybaena pellucida* Kuroda & Habe (hereafter, BP) and *B. similaris* (Rang) (BS) are closely related sibling species (Hirano et al., 2014) that are difficult to separate by shell morphology or gross genital anatomy. They can be clearly distinguished from each other by penile microsculpture or fluorescent mantle pigments, although the latter disappears depending on the environment (Seki et al., 2008). They share common genetic systems of shell banding (Asami et al., 1993) and color (Asami et al., 1997a; Asami and Asami, 2008). Their pre- and post-mating reproductive isolations are incomplete in the laboratory, although they assortatively mate with conspecifics (Wiwegweaw et al., 2009a, b). BP is endemic to Japanese islands, where BS

---

* Corresponding author. Tel. : +81 263 37 2494;
Fax : +81 263 37 2494;
E-mail: asami99@shinshu-u.ac.jp

Supplemental material for this article is available online.
doi:10.2108/zs150020

**Table 1.** Survey sites.

| Region | Site | Latitude (N) | Longitude (E) | Altitude (m) | Site name | Species |
|---|---|---|---|---|---|---|
| North | 1 | 35°34′49″ | 140°40′04″ | 9 | Tama, Togane | *B. similaris* |
| | 2 | 35°34′46″ | 140°22′34″ | 18 | Yamada, Togane | *B. pellucida* |
| South | 3 | 34°59′16″ | 139°51′16″ | 4 | Harbor, Tateyama | *B. similaris* |
| | 4 | 34°59′12″ | 139°51′93″ | 7 | Shiodome-bashi, Tateyama | *B. similaris* |
| | 5 | 34°58′54″ | 139°51′16″ | 20 | Castle west, Tateyama | *B. pellucida* |
| | 6 | 34°58′51″ | 139°51′18″ | 23 | Castle south, Tateyama | *B. pellucida* |
| | 7 | 34°58′51″ | 139°51′24″ | 32 | Castle east, Tateyama | *B. pellucida* |
| | 8 | 34°55′28″ | 139°50′18″ | 20 | Daijinngu, Tateyama | *B. pellucida* |
| | 9 | 34°54′42″ | 139°52′11″ | 28 | Shirahama, Minami-boso | *B. similaris* |

was introduced, presumably several hundred years ago (Komai and Emura, 1995; Asami et al., 1997b). They can be sympatric, but their patchy distributions may be negatively associated with each other (Seki et al., 2002).

We found that BP and BS exhibit discrete patterns of population dynamics despite their close relatedness. The annual life cycle of BP is synchronized whereas BS reproduces in continuous generation. Here we show the contrasting life cycles of BP and BS in the same climatic ranges.

## MATERIALS AND METHODS

We conducted the present survey at nine sites in two regions of the Boso Peninsula, Chiba, Japan from April 2006 to March 2007 (Table 1, Fig. 1), except for site 4, which was not surveyed in April 2006. One region, Togane (hereafter, the north), is about 74 km north of the other region, Tateyama and Minami-Boso (the south). The straight distances between the sites of different regions range from 80 to 90 km. We designed surveys in the two regions to include a test of whether survey results within each region are repeatable between relatively distant regions that are available within the latitude range of the peninsula.

In every survey, we collected living individuals within an area of 3 × 3 m for 15 min. We avoided removing or overturning objects and minimized physical changes to habitats to let each population continue natural life history over the period of repeated surveys. We searched for living BP in an area of approximately 500 m in radius from each site from November to March, when they were not found within the site. According to Seki et al. (1997), we distinguished BP from BS by the presence of yellow pigments. We measured shell widths with vernier calipers and recorded whether each specimen was sexually mature based on the presence of the reflected shell lip. We then returned all the individuals to each site where we collected them.

## RESULTS

The two species were found together at sites 3 and 9, where BS was predominant to BP. In other sites, only one of the two species was found throughout the year. At site 9, the proportion of BP individuals in each sample ranged from 1.9% in October to 18.6% in July. At site 3, only BS was detected over the surveys, except for a single BP individual found in August. Due to the limited abundances, we did not examine population structure of BP at these sites.

In April, we found young juveniles and no adult of BP at sites 7 and 8, where the mean shell widths were 3.5 ± 1.1 mm ($n$ = 3) and 5.7 ± 2.1 mm ($n$ = 13), respectively. Shell width increased gradually from April to October in each population of BP (Fig. 2A). An adult individual of BP was

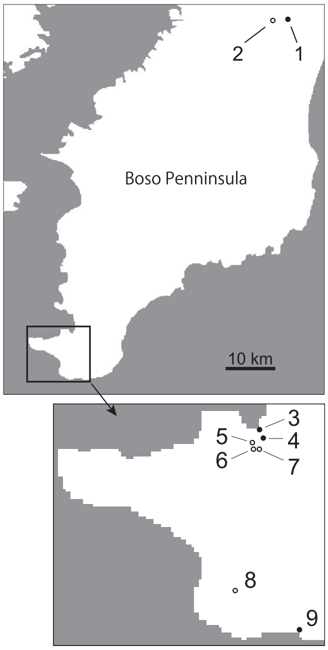

**Fig. 1.** Locations of survey sites, where population dynamics of *Bradybaena pellucida* (open) and *B. similaris* (filled) were examined.

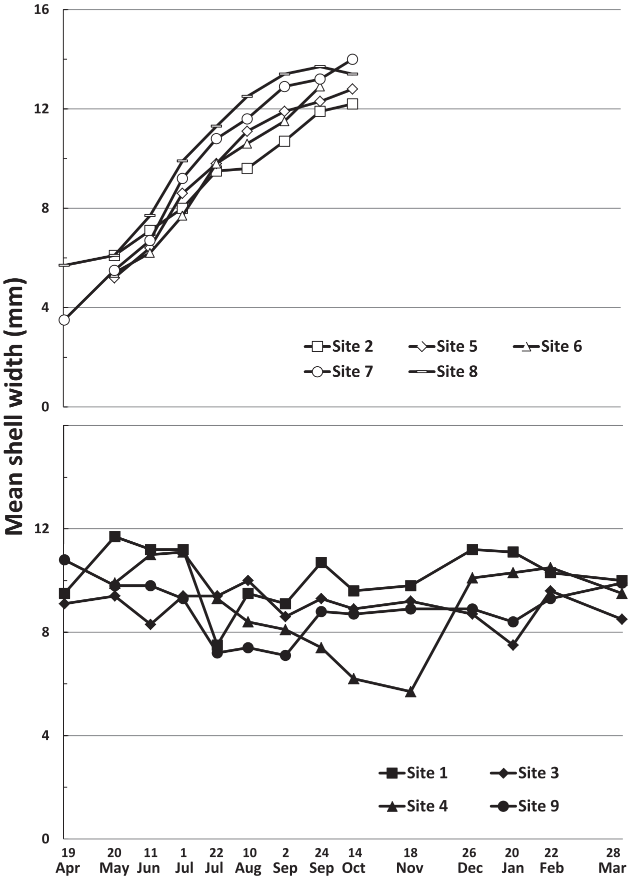

**Fig. 2.** Contrasting seasonal changes of mean shell width in *Bradybaena* species. The horizontal axis indicates each survey time defined as the number of days since 19 April. No individuals of *B. pellucida* were found in surveys from November through March.

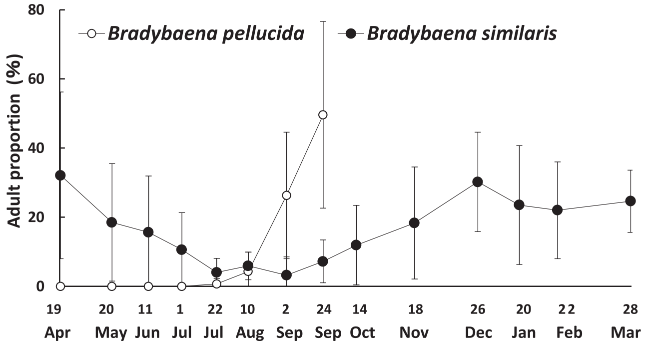

**Fig. 3.** Contrasting seasonal changes of adult proportion in *Bradybaena* species. The mean adult proportion among the survey sites is shown for each species against each survey time in the number of days since the first survey on 19 April.

found for the first time in the year at site 8 on 22 July. The proportion of adults in BP population increased at every site; the mean proportion rose from 4.3% in August to 50.0% in October (Fig. 3). However in late September, relative abundance began to decline rapidly in BP populations in both the south (Fig. 4; Supplementary Figs. S5–S7) and north (Supplementary Fig. S2). In late September and mid-October, the shell of adult BP was often so thin and fragile that it could easily be crushed if picked up by fingers, or was naturally peeling off in pieces. After we recorded eight individuals in total across all the sites of BP in October, we detected no living BP from November through March within the sites and surrounding areas surveyed in the south (Fig. 4; Supplementary Figs. S5–S7) and north (Supplementary Fig. S2).

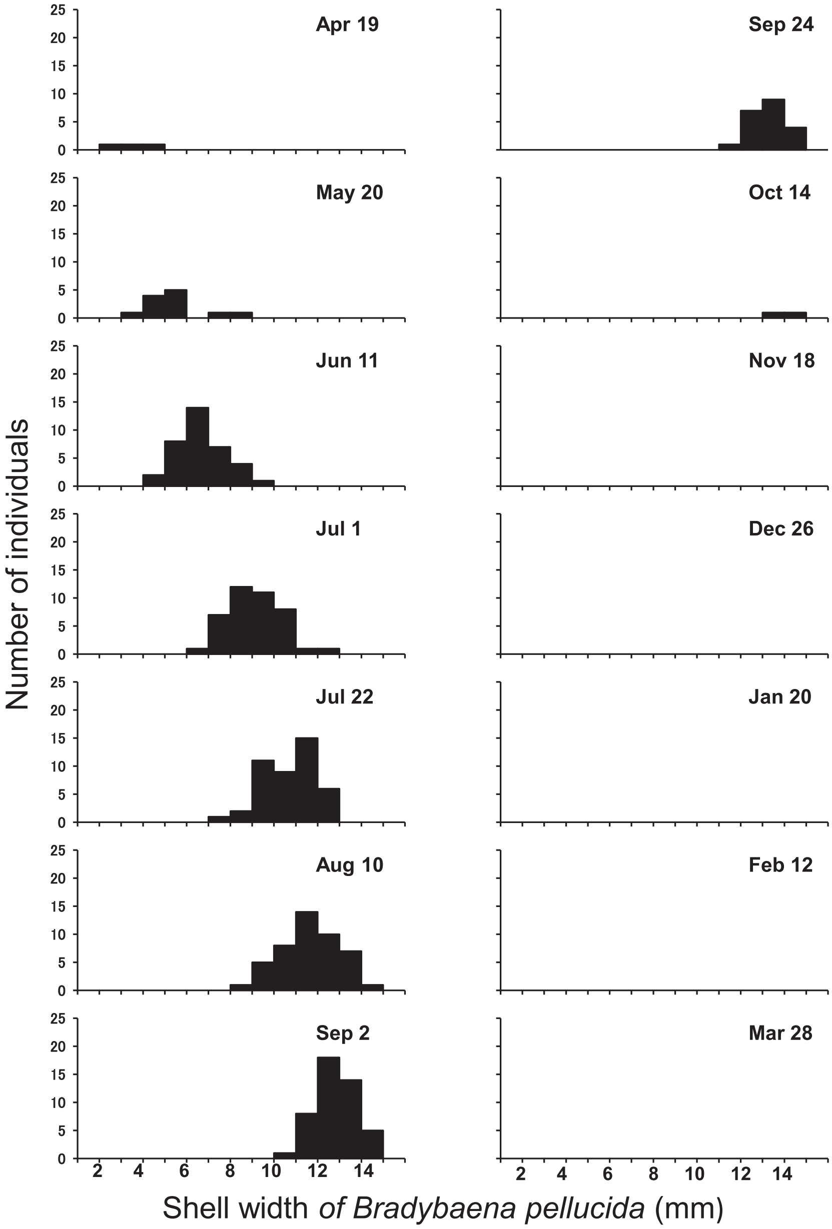

**Fig. 4.** Seasonal change in population size structure of *Bradybaena pellucida* in the south (site 7). No individuals were found in surveys from November through March.

BS exhibited a distinct annual pattern in size and age structure of population, compared with that of BP. There were no consistent increases in mean shell width of BS over the year (Fig. 2B) or in adult proportion (Fig. 3). Similar annual patterns of size structure were observed in both the south (Fig. 5; Supplementary Figs. S3, S4) and north (Supplementary Fig. S1). Unlike those of BP, adults of BS decreased from 32.1% in April to 3.2% in early September in mean across the four sites, but did not become undetectable through the winter. In general, the shell width varied among BS individuals in wide ranges throughout the year (Fig. 5; Supplementary Figs. S1, S3, S4) relative to the ranges in BP populations (Fig. 4; Supplementary Figs. S2, S5–S7; Supplementary Table).

## DISCUSSION

Our results show that the two congeneric species of snails *Bradybaena pellucida* (BP) and *B. similaris* (BS) differ in their life histories and exhibit contrasting annual patterns of population dynamics, despite their close relatedness and morphological similarities. Their differences are consistent between the south (Tateyama and Minami-Boso) and north (Togane) regions in the Boso peninsula, as well as among the sites within these regions. Thus, their interspecific differences in ecology are not ascribable to spatially varying or limited conditions of environment in the present geographical scale of survey.

No adults but only small juveniles of BP were found in mid-April. Their mean shell size, as well as the proportion of adults, continued to increase up to autumn. After we recorded a few remaining individuals in October, we found no living individuals of BP from November through March in the survey sites and surrounding areas. In late September and mid-October, many individuals exhibited darkened body coloration through semitransparent shells. Broken

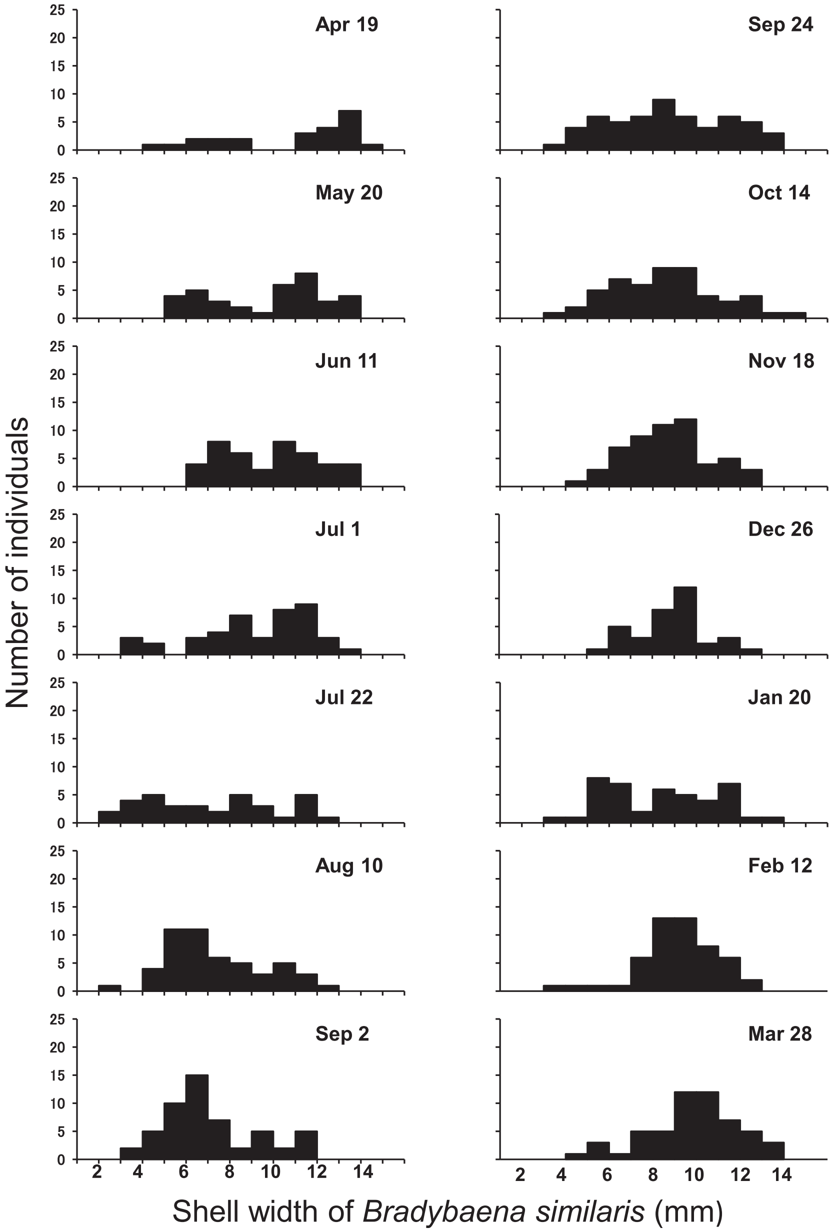

**Fig. 5.** Seasonal change in population size structure of *Bradybaena similaris* in the south (site 9).

pieces of empty shells with the lip in the litter indicated subsequent death. Populations of BP in the present regions are thus annual in life history and semelparous in reproduction. Life history stages are synchronized among BP individuals in populations, which results in discontinuous generation. This life cycle is thus univoltine.

This does not, however, mean that no fraction of population survives winter in the survey sites. The present study instead most probably underestimated the fraction of small juveniles in their populations. We gave priority to minimizing habitat perturbation in each survey, and did not remove the litter layer, which would otherwise have allowed for more thorough searches. Perhaps for this reason we detected only a few or no individuals of around 2 mm shell width, which is the size of hatchlings, throughout the year in BP and BS sites. The absence of detectable individuals after October suggests that populations of BP overwinter in stages of egg and/or young juvenile. Our results thus illuminate the importance of physically thorough searches of the litter layer for small juveniles and egg masses in winter as a further step toward understanding the overwintering ecology of these animals.

The shell of BP is thin and could be sufficiently fragile to break when picked up from the substrate in the field, while this is not the case in BS (Seki et al., 2008). This may make sense for a snail species in which adults do not normally overwinter in terms of reducing the allocation of limiting resources to thicken the shell in an equivalent manner to BS. This hypothesis needs to be testified by further examination of other comparable shelled-pulmonates.

In contrast, populations of BS include individuals of almost all ages from hatchling to sexually matured adults around the year. Even in relatively cold seasons from November to March, more than 20% were adults in every sample. This indicates that both adults and juveniles overwinter in BS populations. In the mean across the four sites of BS, proportions of adults and juveniles did not seasonally shift in a clear direction, in contrast to the increases of mean size and adults in BP populations after spring. Fractions of small juveniles were also found in autumn through winter as well. These results suggest that reproduction continues in BS populations from April or earlier through autumn.

BS individuals collected from Tokyo, Japan reproduced and lived for 284 days after maturity in the mean among four different conditions (Asami and Ohbayashi, 1999). A sample of BS from Juiz de Fora, Brazil lived for 144 days after hatching (Carvalho et al., 2008). The life span of BS in the wild has been reported to be about 12 months in Taiwan (Chang, 2002). These observations support the conclusion that most BS individuals follow an annual life cycle. Unlike BP populations, however, growth and death are not synchronized among individuals, and thus BS reproduces in overlapping generation. These results suggest that annual life history in pulmonates may not necessarily be synchronized among individuals.

In synchronized semelparity, as is exhibited by BP, all adults disappear from populations in a particular season. Thus, only a single cohort composes each population in discontinuous generation. This form of population dynamics is found in slugs of *Arion lusitanicus* (Kozlowski and Sionek, 2000), *Deroceras reticulatum* (Natalia et al., 2008), and snails of *Theba pisana* (Heller, 1982), *Xeropicta arenosa* (Staikou and Lazaridou-Dimitriadou, 1991). Although some populations of *Xeropicta derbentina* (Kiss et al., 2005) and

*Succinea putris* (Kuznik-Kowalska et al., 2013b) exhibit semelparous and annual life histories, it is unclear whether adults disappear in a season. In contrast, similarly to BS, non-synchronized semelparous life history in overlapping generation is found in hygromiid snails *Monacha cartusiana* (Staikou and Lazaridou-Dimitriadou, 1990a) and *Trochulus hispidus* (Kuznik-Kowalska et al., 2013a).

Closely related species such as congeners may differ from one another in life spans. For instance, the life span of *Lymnaea stagnalis* may extend to seven years (Boag et al., 1979) in contrast to the typically annual life cycle of *L. peregra* (Lam et al., 1989). Distinct divergence between synchronous and non-synchronous semelparity within a genus, however, has not to our knowledge been documented before the present study. *Fruticicola fruticum*, which was formerly classified in the genus *Bradybaena*, reproduces over several years (Staikou et al., 1990b). Phylogenetic relations of this iteroparous species to semelparous bradybaenids such as BP and BS remain open to be examined.

Within species, life history could vary depending on environmental conditions (Heller, 2001). For example, terrestrial pulmonates *Xeropicta derbentina* (Kiss et al., 2005), *Xerolenta obvia* (Lazaridou and Chatziioznnou, 2005) and *Theba pisana* (Cowie, 1984; Baker and Vogelzang, 1988) as well as a tidal pulmonate *Salinator takii* (Kosuge, 2000) exhibit either an annual or two-year life cycle. The life span of the pond snail *Lymnaea stagnalis* varies from one to seven years (Boag and Pearlstone, 1979). The discrete patterns of life history between the present species may also vary geographically, for example depending on climate. The present findings thus prompt further studies to quantify the effects of climate on differences in the life histories of these species.

BP and BS differ in their patterns of geographical distribution. Over recent several decades, BP has widened its distribution northeastward by colonizing open lowlands along the pacific side of Honshu island (Asami et al., 1997b; Seki et al., 2002). The study sites in this report are located in the Boso peninsula, which BP colonized most probably in relatively recent times. In contrast, BS has successfully established worldwide distribution with humans in temperate and tropical regions, while BP remained within a range in western Japan (Komai and Emura, 1955; Asami et al., 1997b; Seki et al., 2002). Our results provide a ground to study possible roles of life history in the continuing dynamics of colonization and extinction in the two species. Colonization by BS may have been widely and frequently successful compared to the case of BP due to their contrasting life histories. The recent northward range expansions of BP may have been possible because the recent rises of winter temperature improved its overwintering survival. Our results provide a crucial basis to test these hypotheses.

Among gastropods, the two species studied here are exceptionally easy to breed in a relatively short time (Asami and Ohbayashi, 1999; Wiwegweaw et al., 2009b). Previous studies have demonstrated an array of technical and biological advantages of BP and BS as a pulmonate model system for the field and laboratory studies of ecology, behavior and evolution (Asami et al., 1998; Ueshima and Asami, 2003; Wiwegweaw et al., 2009a; Utsuno and Asami, 2010; Kimura et al., 2014). Our findings of contrasting population dynamics shed light on useful features and questions in the population ecology of these species.

Considering their close relatedness and affinities in morphology and other characteristics (Seki et al., 2008; Wiwegweaw et al., 2009a, b; Hirano et al., 2014), the present results suggest that their annual patterns of population dynamics have relatively recently diverged. Our study demonstrates that closely related sibling species of terrestrial pulmonates can exhibit distinct life histories that are nonetheless similarly adaptive in the same temperate ranges.

## ACKNOWLEDGMENTS

We thank M. Okamoto, K. Seki, N. Asami and M. Asami for their help in the field and B. Páll-Gergely for his help in literature survey. This study was partly supported by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science to N.N. and T.A.

## REFERENCES

Asami T, Asami N (2008) Maintenance mechanism of a supergene for shell colour polymorphism in the terrestrial pulmonate *Bradybaena similaris*. Basteria 72: 119–127

Asami T, Ohbayashi K (1999) Effects of oviposition substrate on lifetime fecundity of the terrestrial pulmonate *Bradybaena similaris*. J Conch 36: 1–8

Asami T, Fukuda H, Tomiyama K (1993) The inheritance of shell banding in the land snail *Bradybaena pellucida*. Venus 52: 155–159

Asami T, Ohbayashi K, Seki K (1997a) The inheritance of shell Color in the land snail *Bradybaena pellucida*. Venus 56: 35–39

Asami T, Yamasita H, Park J, Ishikawa H (1997b) Geographical distributions of the land snail *Bradybaena pellucida* (Pulmonata: Bradybaenidae). Yuriyagai 5: 31–42

Asami T, Ohbayashi K, Cowie R (1998) Evolution of Mirror Images by Sexually Asymmetric Mating Behavior in Hermaphroditic Snails. Am Nat 152: 225–236. DOI: 10.1086/286163

Asami T, Seki K, Inoue S (2002) Geographical distributions of sibling species of snail *Bradybaena pellucida* and *B. similaris* in the Boso Peninsula. Venus 61: 41–48

Baker GH, Vogelzang BK (1988) Life history, population dynamics and polymorphism of *Theba pisana* (Mollusca: Helicidae) in Australia. J Appl Ecol 25: 867–887

Boag DA, Pearlstone PSM (1979) On the life of *Lymnae stagnalis* (Pulmonata: Gastropoda) in southwestern Alberta. Can J Zool 57: 353–362. DOI: 10.1139/z79-041

Carvalho CDM, Bessa ECDA, D'Ávila S (2008) Life history of *Bradybaena similaris* (Mollusca, Pulmonata, Bradybaenidae). Moll Res 28: 171–174

Chang CP (2002) *Bradybaena similaris* (de Férussac) (Bradybaenidae) as a pest on grapevines of Taiwan. In "Molluscs as Crop Pests" Ed by GM Barker, CABI Publishing, New York, pp 241–244

Cowie RH (1984) The Life-cycle and productivity of the land snail *Theba pisana* (Mollusca: Helicidae). J Anim Ecol 53: 311–325

Heller J (1982) National history of *Theba pisana* in Israel (Pulmonata: Helicidae). J Zool Lond 196: 475–487

Heller J (1990) Longevity in Mollscus. Malacologia 31: 259–295

Heller J (2001) Life history strategies. In "The Biology of Terrestrial Molluscs" Ed by GM Barker, CABI Publishing, London, pp 413–445

Hirano T, Kameda Y, Chiba S (2014) Phylogeny of the land snails *Bradybaena* and *Phaeohelix* (Pulmonata: Bradybaenidae) in Japan. J Mollus Stud 80: 177–183. DOI: 10.1093/mollus/eyu004

Hughes PW, Simons AM (2014) The continuum between semelparity and iteroparity: plastic expression of parity in response to season length manipulation in *Lobelia inflata*. BMC Evol Biol 14: 90. DOI: 10.1186/1471-2148-14-90

Kimura K, Hirano T, Chiba S (2014) Assortative mating with respect to size in the simultaneously hermaphroditic land snail *Bradybaena pellucida*. Acta Ethol. DOI: 10.1007/s10211-014-0211-7

Kirkendall LR, Stenseth NC (1985) On defining “Breeding Once”. Am Nat 125: 189–204

Kiss L, Labaune G, Magnin F, Aubry S (2005) Plasticity of the life cycle of *Xeropicta derbentina* (Krynicki,1836), a recently introduced snail in Mediterranean France. J Moll Stud 71: 221–231. DOI: 10.1093/mollus/eyi030

Komai T, Emura S (1955) A study of population genetics of the polymorphic land snail *B. similaris*. Evolution 9: 400–418

Kosuge T (2000) Seasonal aspects in the life history and ecology of the intertidal Pulmonata *Salinator takii* Kuroda (Gastropoda: Amphibolidae). Venus 59: 19–28

Kozlowski J, Sionek R (2000) Seasonal fluctuations of abundance and age structure of *Arion lusitanicus* Mabille, 1868 (Gastropoda: Pulmonata: Arionidae). Fol Malac 8: 271–276

Kramarenko SS (2013) The analysis of the reproductive traits of the pulmonate molluscs: a mini-review. Ruthenica 23: 115–125

Kuznik-Kowalska E, Prockow M, Drvotova M, Jurickova L (2013a) Field and laboratory studies on the life-cycle, growth and feeding preference in the hairy snail *Trochulus hispidus* (L., 1758) (Gastropoda: Pulmonata: Hygromiidae) Biologia 68: 131–141

Kuznik-Kowalska E, Pokryszko M, Prockow M, Oczkowska M (2013b) On the population dynamics, reproductive biology and growth of *Succinea putris* (Linnaeus, 1758) (Gastropoda: Pulmonata: Succineidae). Fol Malac 21: 215–224

Lam PKS, Calow P (1989) Intraspecific life-history variation in *Lymnaea peregra* (Gastropoda: Pulmonata) I. field study. J Anim Ecol 58: 571–588

Lazaridou M, Chatziioannou M (2005) Differences in the life histories of *Xerolenta Obvia* (Menke, 1828) (Hygromiidae) in a coastal and a mountainous area of northern Greece. J Moll Stud 71: 247–252. DOI: 10.1093/mollus/eyi032

Maltz TK (2003) Life cycle and population dynamics of *Helicodota obvoluta* (O. F. Müller, 1774) (Gastropoda: Pulmonata: Helicidae) Fol Malac 11: 63–88

Natalia LC, Alicia NL, Maria GM, Nestor JC, Pablo LM (2008) Biological studies and phenology of the slug *Deroceras reticulatum* (Müller, 1774) (Pulmonata: Stlommatophora). Inv Rep Dev 52: 23–30

Pokryszko BM (2001) Observations on seasonal dynamics of age structure and reproduction of *Pupilla muscorum* L. (Gastropoda: Pulmonata: Pupillidae). Fol Malac 9: 45–50

Roff DA (1992) The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York

Seki K, Inoue S, Asami T (2002) Geographical distribution of sibling species of snail *Bradybaena pellucida* and *B. similaris* in the Boso Peninsula. Venus 61: 41–48

Seki K, Wiwegweaw A, Asami T (2008) Fluorescent pigment distinguishes between sibling snail species. Zool Sci 25: 1212–1219. DOI: http://ddoi.org/10.2108/zsj.25.1212

Staikou A, Lazaridou-Dimitriadou M (1990a) Aspect of the life cycle, population dynamics, growth and secondary production of the snail *Monacha Cartusiana* (Müller, 1774) (Gastropoda Pulmonata) in Greece. Malacologia 31: 353–362

Staikou A, Lazaridou-Dimitriadou M, Pana E (1990b) Aspect of the life cycle, population dynamics, growth and secondary production of the snail *Bradybaena fruticum* (Müller, 1774) (Gastropoda Pulmonata) in northern Greece. J Moll Stud 56: 137–146. DOI: 10.1093/mollus/56.2.137

Staikou A, Lazaridou-Dimitriadou M (1991) The life cycle, population dynamics, growth and secondary production of the snail *Xeropicta arenosa* Ziegler (Gastropoda: Pulmonata) in northern Greece. Zool J Linnn Soc 101: 179–188. DOI: 10.1111/j.1096-3642.1991.tb00892.x

Ueshima R, Asami T (2003) Single-gene speciation by left-right reversal. Nature 425: 679. DOI: 10.1038/425679a

Wiwegweaw A, Seki K, Mori H, Asami T (2009a) Asymmetric reproductive *isolation* during simulaneous reciprocal mating in pulmonates. Biol Lett 5: 240–243. DOI: 10.1098/rsbl.2008.0714

Wiwegweaw A, Seki K, Utsuno H, Asami T (2009b) Fitness consequences of reciprocally asymmetric hybridization between simultaneous hermaphrodites. Zool Sci 26: 191–196. DOI: http://dx.doi.org/10.2108/zsj.26.191

Young TP (2010) Semelparity and Iteroparity. Nat Educ Knowl 3: 2

(Received February 10, 2015 / Accepted April 6, 2015)