Evolutionary Ecology Research, 2013, **15**: 933–946

Trophic niche divergence reduces survival in an omnivorous rodent

Pei-Jen L. Shaner[1], Sheng-Hai Wu[2], Linhua Ke[1] and Shuh-Ji Kao[3]

[1]Department of Life Science, National Taiwan Normal University, Taipei, Taiwan,
[2]Department of Life Sciences, National Chung Hsing University, Taichung City, Taiwan and
[3]Research Center for Environmental Changes, Academia Sinica, Taipei, Taiwan

ABSTRACT

Hypothesis: Individuals that diverge from their population's mean trophic niche suffer reduced survival.

Organism: The Taiwan field mouse, *Apodemus semotus*, a common, small, omnivorous rodent.

Field site: *Pinus–Alnus–Quercus* forest in central Taiwan (121°18′E, 24°21′N).

Methods: We used capture–recapture data to measure the survival of individual *Apodemus semotus*. We measured individual trophic niches using stable carbon and nitrogen isotope values obtained from samples of the rodents' hair. We used stepwise logistic regression to evaluate whether an individual's survival depended on the divergence of its trophic niche from the population mean. We controlled for the potentially confounding effects of resource abundance with dry weights of seeds and arthropods collected in seed traps and pitfall traps.

Conclusions: The probability of survival declined with increasing niche divergence from the population mean. Stabilizing selection in this population of *Apodemus semotus* is thus acting to conserve niche width and location.

Keywords: *Apodemus semotus*, trophic niche, stabilizing selection, stable isotopes.

INTRODUCTION

Niche evolution controls biodiversity from ecological to evolutionary time scales. From an ecological perspective, niches underpin species interactions and community structures; from an evolutionary perspective, niches are phenotypes that natural selection can act upon. Theory predicts that evolution tends to conserve the mean phenotype of a population through time (e.g. Holt and Gaines, 1992; Holt and Gomulkiewicz, 1997). However, recent studies have provided empirical evidence on rapid divergence in trophic niches through disruptive selection within populations (Bolnick, 2004; Hendry *et al.*, 2009; Martin and Pfennig, 2009) or divergent selection among populations (Knudsen *et al.*, 2006; McCormack and Smith, 2008). On the one hand, trophic niche is strongly influenced by ecological conditions such as competitors and food

---

Correspondence: P.-J.L. Shaner, Department of Life Science, National Taiwan Normal University, 88 Tingzhou Road, Sec. 4, Taipei 11677, Taiwan. e-mail: pshaner@ntnu.edu.tw

availability. These conditions change rapidly in space and time, which should promote a divergent trophic niche and rapid evolution of its related traits. On the other hand, feeding adaptations often involve many coordinated traits (e.g. foraging behaviour, metabolism, digestibility), which tend to slow down evolution. Therefore, depending on the relative strengths of these influences, trophic niches may be divergent or conserved.

Trophic niches can be measured at various resolutions, from food size [e.g. different gill raker lengths (Bolnick, 2004)] to food type [e.g. pine cones vs. acorns (McCormack and Smith, 2008)] and trophic level [e.g. omnivory vs. carnivory (Martin and Pfennig, 2009)]. Therefore, fitness consequences of individual differences from the population's mean trophic position can vary depending on the resolution of trophic niche. For instance, individuals may gain fitness as they diverge from the population's mean trophic niche under strong intraspecific competition. An individual feeding on a diet different from others in the population may gain fitness through reduced food competition (Martin and Pfennig, 2009) or as it diverges towards higher trophic levels with increased nitrogen intake (Bowen *et al.*, 1995; Denno and Fagan, 2003). Fitness may decline, however, if a divergent niche fails to meet nutritional requirements (Lewis *et al.*, 2001; Mayntz *et al.*, 2005) or when the trade-offs between diet breadth and competitive ability (Ackermann and Doebeli, 2004) limit individuals' ability to compete with heterospecific trophic specialists (Martin and Pfennig, 2009). Therefore, a range of phenotype–fitness relationships may exist for trophic niche, including disruptive, directional or stabilizing selection.

In this study, we measure the survival and trophic niche of the Taiwan field mouse (*Apodemus semotus*). We use the relationship between survival and divergence of individual niches from the population mean to infer selection. Survival may be higher for individuals with increased niche divergence, suggesting disruptive or directional selection and the species' ability to expand niche width or shift niche position. Alternatively, survival may be lower for individuals with increased niche divergence, suggesting stabilizing selection and the conservatism of the species' niche.

We use stable carbon and nitrogen isotope values (δ^{13}C ‰, δ^{15}N ‰) to quantify each individual's trophic niche (Post, 2002). Specifically, δ^{13}C values can reflect dietary carbon sources such as C3 plants versus C4 plants (Newsome *et al.*, 2007), whereas δ^{15}N values generally increase with trophic level (reviewed by Vanderklift and Ponsard, 2003). Isotope values have been used to demonstrate rapid dietary shifts in omnivorous rodents experiencing resource fluctuations (Stapp *et al.*, 1999; Shaner and Macko, 2011), suggesting that disruptive selection for trophic divergence is likely in omnivorous rodents. However, changes in δ^{15}N values frequently involve dietary shifts across trophic levels, which could trigger foraging constraints such as increased need to balance nutrients, or reduced efficiency from competing against trophic specialists. Therefore, it is difficult to infer selection for trophic divergence from observations of dietary shifts alone. Fitness consequence of persistent trophic divergence by omnivorous rodents needs to be evaluated in order to infer selection operating on their trophic niche.

We used a capture–recapture data set to measure rodent survival as a function of trophic divergence. Survival and trophic divergence were used as proxies to an individual's fitness and phenotype respectively. Our predictions are:

1. If trophic divergence is adaptive, individuals with divergent diets should attain similar, or even higher, survival than individuals whose diets are closer to the population mean.
2. If trophic niche is conserved, individuals with divergent diets should suffer lower survival than individuals whose diets are closer to the population mean.

Resource abundance may independently influence survival and trophic niche, creating a spurious relationship between survival and trophic divergence. For instance, low resource abundance could lead to starvation, which decreases survival and forces individuals to feed more opportunistically, resulting in divergent diets. Therefore, we also included resource abundance, measured with dry weights of seeds and arthropods, in the survival function to control for its potentially confounding effects on the relationship between survival and trophic divergence.

MATERIALS AND METHODS

Study system and sampling design

Apodemus semotus is a small (~27 g) murid rodent commonly found in forests and grasslands in the montane region of Taiwan (Yu, 1993), including our study site in a *Pinus–Alnus–Quercus* forest (121°18′E, 24°21′N). Based on a 15-month study of an *A. semotus* population around 35 km from the study site, individuals reproduce twice each year in spring and fall. Females were found to have no more than two sets of placental scars [i.e. maximum number of pregnancies is two (Huang *et al.*, 1997)], suggesting a life span in the wild of approximately one year.

We assessed selection on the trophic niche of *A. semotus* in three sampling grids, each comprising 64 trapping stations in an 8 × 8 array with 10 m between stations. Adjacent grids were 60 m apart. The sampling had three components: rodent trapping for survival estimates, hair sampling for trophic niche estimates, and samplings of seeds and arthropods for resource abundance estimates (Fig. 1).

Rodent survival

We performed six bi-monthly trapping sessions beginning in August 2010 and ending in June 2011 for a total of 10 months (Fig. 1). Each trapping session comprised three consecutive days. Upon first capture, each rodent was marked with an ear-tag for individual identification, and a small hair sample was taken for stable isotope analysis (see ‘Trophic divergence’ below). Hair samples were also taken from recaptured individuals if their previously cut hair had fully re-grown. The rodents were immediately released after processing at the station where they were captured.

Of the 75 individuals that were first captured in August 2010 and tracked for the entire 10-month period, only 22 were ever recaptured (Fig. 2). Of these, 95% (21 of 22) were recaptured within 2 months and 100% recaptured within 6 months. Therefore, we estimated rodent survival over a fixed 6-month period. Specifically, survival of the August-captured cohort was based on those known alive anytime between October and February, the October-captured cohort on those alive anytime between December and April, and the December-captured cohort on those alive anytime between February and June (Fig. 1). Because only a small proportion of the individuals were still being recaptured after the initial 2-month period, we combined all recapture records within the 6-month period to provide a binomial survival estimate. If an individual was recaptured anytime within the 6-month period, it was alive for 2–6 months and its survival was recorded as 1; otherwise, it was recorded as 0. Each unique rodent had only one survival record.

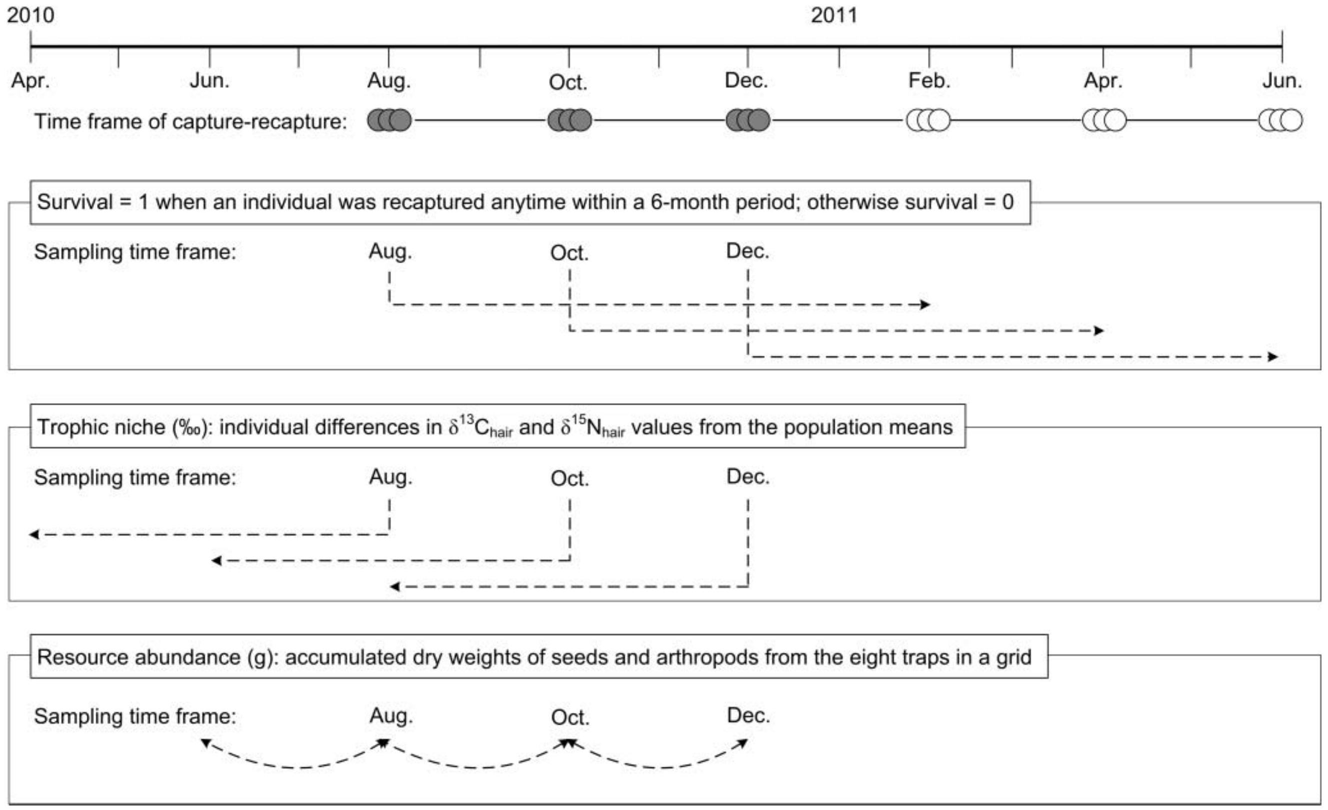

Fig. 1. Methodology roadmap. The timeline on top of the diagram provides reference to different sampling events. The bi-monthly trapping of *Apodemus semotus* began in August 2010 and ended in June 2011. Each of the six trapping sessions comprised three consecutive days (each circle denotes one day). The data analysed in this study were based on *A. semotus* captured between August and December 2010 (filled circles). The dashed lines indicate the approximate time frame that a sample represents. The text boxes provide brief descriptions of the estimates on rodent survival, rodent trophic niche, and resource abundance derived from different sampling events.

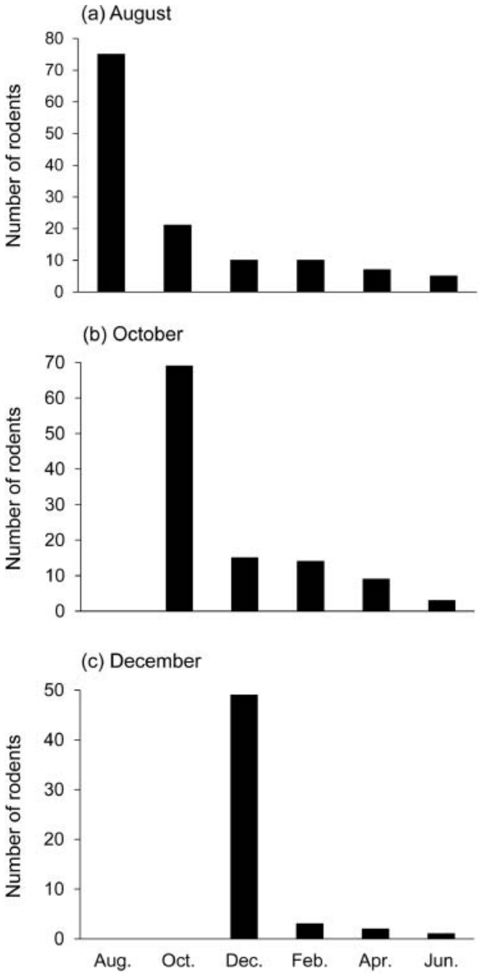

Fig. 2. Frequency distributions of *Apodemus semotus* capture history. The trapping began in August 2010 and ended in June 2011 for a total of six trapping sessions over a period of 10 months. Recapture of animals first caught in August (a), October (b), and December (c) was assessed through June 2011. The complete capture history of *A. semotus* is provided in Table S2 (see evolutionary-ecology.com/data/2796Appendix.pdf).

Although capture–recapture data do not provide direct measures of survival, recapture is a reasonable indicator of survival in our study. The study site was on a river terrace, isolated from other forested areas by rivers, paved roads, and orchards. Therefore, emigration out of the study site may be risky for these small rodents. Furthermore, we trapped *A. semotus* more intensively at the same site from May to September 2013 for a separate project. We increased effort to 3-day trapping sessions every 2–4 weeks, with a total of 300 trapping stations that covered the entire river terrace, including the three grids used in this study. Capture history of animals in 2013 was similar to the pattern reported here (P.L. Shaner, unpublished data). Of the 150 individuals first captured in May 2013, 79 were recaptured by September. Seventy-eight of these animals were recaptured by July, and only 19% (15 of 79) were still being recaptured in September. These data collected over a much larger spatial extent strongly suggest mortality or permanent emigration when an individual was not recaptured. Nevertheless, survival estimates based on capture–recapture data are best considered "apparent" survival.

Resource abundance

Seeds and arthropods represent two of the three most frequent dietary items in the fecal samples of *A. semotus* (Lin and Shiraishi, 1992). Therefore, we used their dry weights as the measures of resource abundance in this study. Mycophagy is also commonly observed in omnivorous mammals (Claridge and May, 1994; Claridge *et al.*, 1999; Mangan and Adler, 2000), including *A. semotus* (Lin and Shiraishi, 1992). The extensive soil surveys necessary to obtain reliable estimates of fungi abundance (e.g. Lehmkuhl *et al.*, 2004) were beyond the scope of our study, so we were unable to provide abundance data on fungi comparable to that on seeds and arthropods.

We set eight pairs of seed and pitfall traps at eight randomly selected locations within each of the three grids in June 2010. We erected 1-m^2 seed traps made from mesh netting at a height of 1 m above the ground. Pitfall traps were plastic cups (diameter = 6.5 cm, height = 4.8 cm) filled with ~50 mL of a formaldehyde–glycerin–water solution in ratios of 2:1:7 respectively. The pitfall traps were buried at a depth such that the top of the cup was flush with the surface of the ground. The distance between any two locations of seed and pitfall traps was more than 10 m. We collected seeds and arthropods in August, October, and December. Each collection was thus composed of biomass accumulated over the previous 2 months (Fig. 1).

Storms damaged two seed traps in October and one in December, as well as one pitfall trap in October and three in December, leaving a total of 69 and 68 samples of seeds and arthropods respectively. We separated seeds from the rest of the litterfall collected in the seed traps, which was mainly composed of leaves and twigs, and measured the dry weights of both components. The dry weights of the seeds and the remaining litterfall were positively correlated ($r_s = 0.39$, $P = 0.001$, $N = 69$). However, the dry weights of the arthropods collected at the same locations were not correlated with either seed dry weights or litterfall dry weights ($P > 0.1$). Thus, we used total dry weight of seeds or arthropods from the eight traps in a grid as our estimate of local resource abundance for those individual rodents captured in the same grid during the same trapping session.

Trophic divergence

Stable carbon and nitrogen isotope values (δ^{13}C ‰, δ^{15}N ‰) provide information on assimilated food that accumulates in the diet over a period from days to an animal's lifetime, depending on the type of tissues analysed (Post, 2002).

For mammalian species that moult annually, hair isotope values infer seasonal diets (e.g. Roth, 2002; Darimont *et al.*, 2009). *Apodemus semotus* does not appear to moult seasonally, and our field records suggest gradual re-growth of previously cut hair within 4 months (P.L. Shaner, personal observation). Therefore, we assume hair isotope values of *A. semotus* reflect a diet accumulated over several months. We used two data sets to check this assumption. First, we compared hair isotope values of six individuals that we had repeatedly captured in August, October, and December. While their δ^{15}N values were similar across trapping sessions (ANOVA, $F_{2,5} = 0.51$, $P = 0.63$; mean ± s.e.: $\delta^{15}N_{August} = 6.7 \pm 0.4‰$, $\delta^{15}N_{October} = 6.8 \pm 0.4‰$, $\delta^{15}N_{December} = 7.2 \pm 0.9‰$), their $\delta^{13}C$ values varied over time ($F_{2,5} = 9$, $P = 0.02$; $\delta^{13}C_{August} = -23.4 \pm 0.2‰$, $\delta^{13}C_{October} = -23.6 \pm 0.2‰$, $\delta^{13}C_{December} = -24.0 \pm 0.2‰$), suggesting that hair tissues could reflect some aspects of dietary changes accumulated over several months. Second, because $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissues in *Mus musculus* are known to reach equilibrium with the isotope values of the food by day 84 and day 112 respectively (MacAvoy *et al.*, 2005), we compared the isotope values of muscle and hair tissues taken from eight individuals that died accidentally in the traps during the study (four from August to December 2010, and four from a preliminary trapping in June 2010). The hair and muscle tissues of those animals had similar isotope values (ANOVA, $\delta^{13}C$: $F_{1,7} = 4.31$, $P = 0.08$; $\delta^{13}C_{hair} = -23.3 \pm 0.5‰$, $\delta^{13}C_{muscle} = -23.8 \pm 0.4‰$; $\delta^{15}N$: $F_{1,7} = 0.58$, $P = 0.47$; $\delta^{15}N_{hair} = 6.0 \pm 0.9‰$, $\delta^{15}N_{muscle} = 5.3 \pm 0.5‰$). Although this is not a direct test of isotope turnover in hair tissues, it showed that hair and muscle tissues would have given similar dietary information on an individual.

To describe the range of variation in the isotope values of potential food sources for *A. semotus* at the study site, we collected tissues for stable isotope analysis from 17 species of C3 plants, one species of C4 plant, eight fungus morphospecies, and six arthropod taxa (Table S1, see evolutionary-ecology.com/data/2796Appendix.pdf). All samples were kept frozen prior to oven drying at 60°C for 48–72 h. The isotopic compositions were measured with a ThermoFinnigan Delta Plus Advantage Isotope Ratio Mass Spectrometer (Bremen, Germany).

We analysed hair isotope values of 100 unique *A. semotus* representing 52% of the total of 193 individuals captured between August and December (Fig. 1). The complete capture history of all 193 individuals is provided in Table S2 (see evolutionary-ecology.com/data/2796Appendix.pdf). One hair sample was used for each individual, taken from the trapping session when it was first captured.

We estimated the degree of an individual's trophic divergence by calculating the Euclidean distance of its isotope values from the population mean on the $\delta^{13}C$–$\delta^{15}N$ bi-plot:

$$\mathrm{sqrt}[(\delta^{13}C_{individual} - \delta^{13}C_{population\ mean})^2 + (\delta^{15}N_{individual} - \delta^{15}N_{population\ mean})^2]\ (‰)$$

where $\delta^{13}C_{population\ mean}$ and $\delta^{15}N_{population\ mean}$ are the means of the 100 individual *A. semotus* pooled across trapping sessions and grids; $\delta^{13}C_{individual}$ and $\delta^{15}N_{individual}$ are the isotope values of each individual. In addition to trophic divergence, we also estimated directional differences in $\delta^{13}C$ and $\delta^{15}N$ values between an individual and the population mean (i.e. $\delta^{13}C_{individual} - \delta^{13}C_{population\ mean}$ and $\delta^{15}N_{individual} - \delta^{15}N_{population\ mean}$), which can be positive or negative depending on whether an individual has higher or lower isotope values than the population mean. These directional differences in isotope values, when merged with our survival estimates, help reveal if directional selection is acting on the trophic niche. Because these two directional differences were also used to calculate Euclidean distance, we performed additional tests to evaluate the effect of trophic divergence on rodent survival independent of these two directional differences.

Statistical analyses

We tested the differences in $\delta^{13}C$ and $\delta^{15}N$ values of *A. semotus* across the three trapping sessions using ANOVA, with trapping grid as a random factor. We tested associations between trophic divergence in *A. semotus* and seed dry weight or arthropod dry weight using Spearman correlations. We used stepwise logistic regression to evaluate the effects of trophic divergence, carbon difference ($\delta^{13}C_{\text{individual}} - \delta^{13}C_{\text{population mean}}$), nitrogen difference ($\delta^{15}N_{\text{individual}} - \delta^{15}N_{\text{population mean}}$), seed dry weight, arthropod dry weight, trapping session, and grid on *A. semotus* survival. Because trophic divergence was calculated with carbon and nitrogen differences, we used two approaches to check if any potential effect of trophic divergence on rodent survival was independent of carbon and nitrogen differences. First, we forced the entry of carbon and nitrogen differences with forward selection into the regression model, and then evaluated the effects of the remaining factors at the 0.05 significance level. Second, we compared Receiver Operating Characteristic (ROC) curves of four models, each containing the intercept plus: carbon difference, nitrogen difference, carbon and nitrogen differences, or trophic divergence. A model that provides appropriate fit to the data should have a smaller Akaike Information Criterion (AIC) than the intercept-only model, with its ROC above 0.5 (i.e. ROC = 0.5 indicates a random guess). The type I error was set at 0.05. All statistics were performed in SAS 9.3.

RESULTS

Resource abundances varied in space and time. The dry weights of seeds and arthropods per grid ranged from 8 to 52 g and from 1 to 3 g respectively (Fig. 3). Seed abundance was generally higher in October and December whereas arthropod abundance was more stable across trapping sessions (Fig. 3). Furthermore, seed and arthropod abundances were more equally distributed among trapping grids in August than in October or December (Fig. 3). The $\delta^{13}C$ and $\delta^{15}N$ values of *A. semotus* were similar across trapping sessions ($\log_{10}$-transformed $\delta^{13}C$: $F_{2,95} = 1.36$, $P = 0.26$; $\log_{10}$-transformed $\delta^{15}N$: $F_{2,95} = 0.00$, $P = 0.995$) (Fig. 4b–d). Pooling across trapping sessions and grids, the population's mean $\delta^{13}C$ and $\delta^{15}N$ values were −23.6 ± 0.1‰ and 5.4 ± 0.3‰ respectively, suggesting that these rodents might feed heavily on arthropods and/or fungi and derive more of their carbon from C3 plants (Fig. 4a). Individual differences in $\delta^{13}C$ values from the population mean were generally smaller compared with their differences in $\delta^{15}N$ values (Fig. 5a, b). Trophic divergence of *A. semotus* ranged from 0.2‰ to 7.4‰ (Fig. 5c). Trophic divergence was not associated with either seed dry weight ($P = 0.17$) or arthropod dry weight ($P = 0.89$).

The only factor entering the logistic regression of rodent survival was trophic divergence. Survival decreased with increasing trophic divergence (Fig. 5d). Other factors, including carbon and nitrogen differences, seed and arthropod dry weights, and trapping sessions and grids, did not pass the stepwise inclusion at the 0.05 significance level. Even when carbon and nitrogen differences were forced into the regression model, trophic divergence was included in the final model (Table S3; see evolutionary-ecology.com/data/2796Appendix.pdf). Furthermore, among the four models (i.e. carbon difference, nitrogen difference, carbon and nitrogen differences, trophic divergence) that we evaluated for data fit, the trophic-divergence model was the only one with an AIC smaller than the intercept-only model and a ROC above 0.5 (Table S4 and Fig. S1; see evolutionary-ecology.com/data/2796Appendix.pdf).

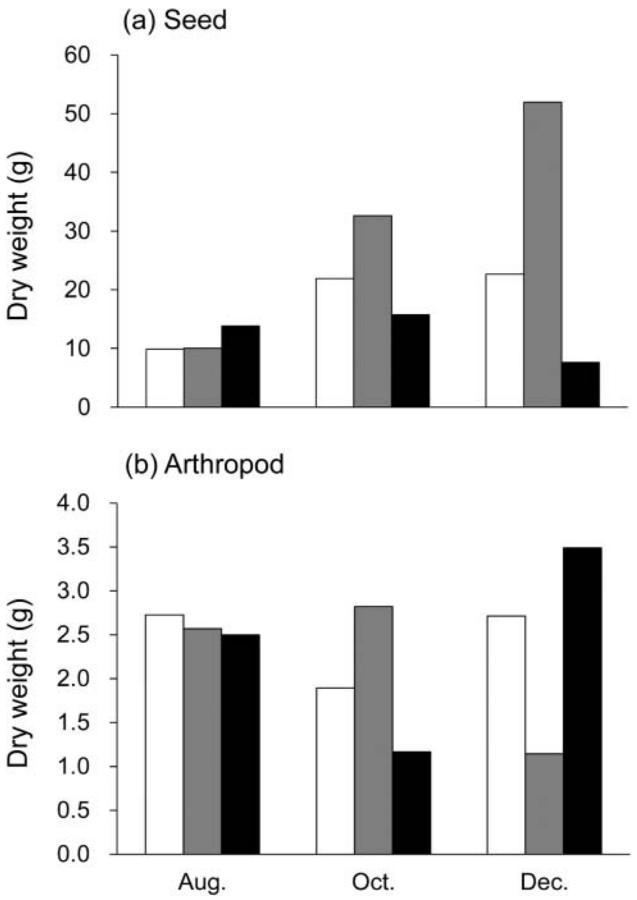

Fig. 3. Seed and arthropod abundances at the study site collected between August and December 2010. Total dry weights of seeds (a) or arthropods (b) were the sums of the eight traps within a grid for a given trapping session. The white, grey, and black bars denote the three trapping grids, labelled A, B, and C respectively in Table S2 (see evolutionary-ecology.com/data/2796Appendix.pdf).

DISCUSSION

Here we report an empirical case of stabilizing selection on trophic niche in a common, omnivorous rodent, *A. semotus*. Specifically, individuals diverging from the population mean trophic position, as quantified by Euclidean distance on the $\delta^{13}C$–$\delta^{15}N$ bi-plot, had lower probability of survival. The stabilizing selection in this population of *A. semotus* is thus acting to conserve the width and location of their trophic niche, adding a counter-example to recent reports on adaptive trophic divergence (Bolnick, 2004; Hendry *et al.*, 2009; Martin and Pfennig, 2009).

The niche concept can be separated into two classes, the Grinnellian niche that drives the large-scale geographic distribution of species, and the Eltonian niche that focuses on resource–consumer interactions at more local scales (Soberón 2007). Because niche evolution can differ as a function of the spatial scale of environmental variation (Holt, 2009), niche axes

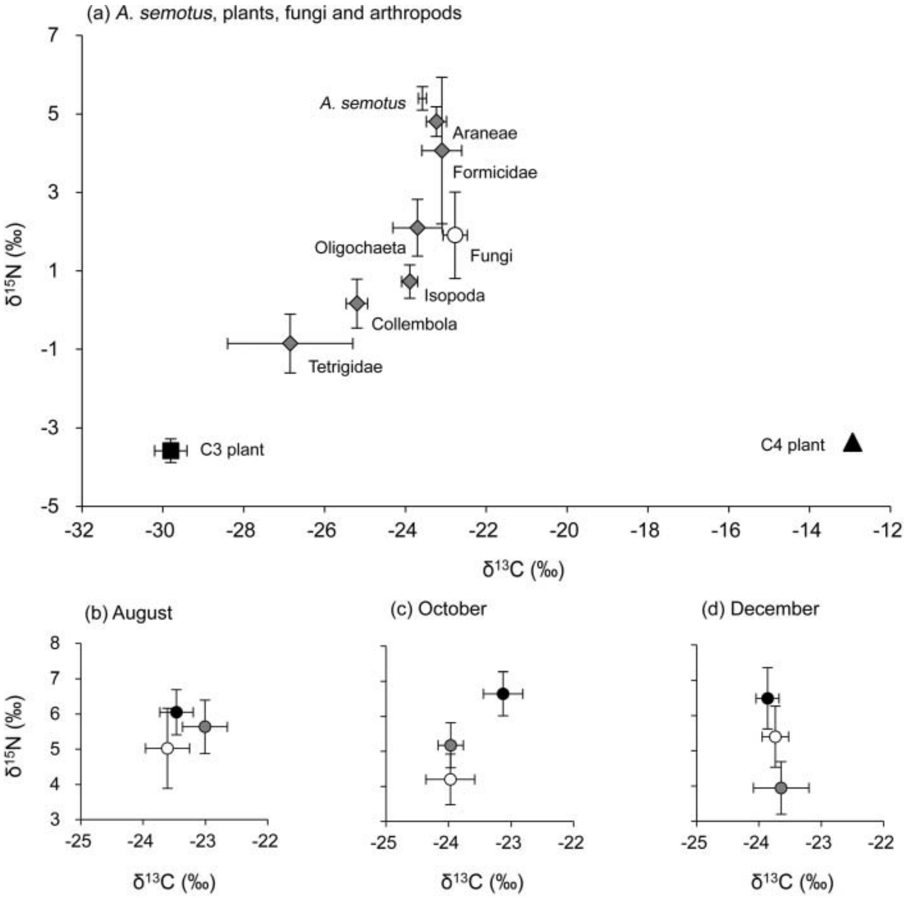

Fig. 4. Stable carbon and nitrogen isotope values of *Apodemus semotus* and their potential food sources. The text labels indicate taxonomic groups. The error bars denote standard errors. The mean isotope values of *A. semotus* are based on 100 individuals in (a). The mean isotope values of *A. semotus* captured in August (b), October (c), and December (d) are given for each grid. The white, grey, and black circles (b–d) denote the three trapping grids, labelled A, B, and C respectively in Table S2 (see evolutionary-ecology.com/data/2796Appendix.pdf). The sample sizes are 12, 14, and 14 for grid A, B, and C respectively in August (b), 11, 12, and 11 for grid A, B, and C respectively in October (c), and 11, 7, and 8 for grid A, B, and C respectively in December (d). The square denotes the mean isotope values of C3 plants (17 species); the triangle denotes the isotope values of C4 plants (one species); the open circle denotes the mean isotope values of fungi (eight morphospecies); the diamonds denote the mean isotope values of each of the six arthropod taxa (2–21 individuals per taxon). Taxon-specific isotope values are provided in Table S1 (see 2796Appendix.pdf).

that vary at finer spatial scales can facilitate rapid niche evolution. Furthermore, while the fundamental niche can be highly conserved (Holt and Gaines, 1992), the realized trophic niche that is being measured in most studies is strongly modified by biotic interactions. As a result, one may expect rapid evolution of trophic-related phenotypes and adaptive trophic divergence, such as in the case of gill raker length in sticklebacks (Bolnick, 2004), beak size in Darwin's finches (Hendry *et al.*, 2009), and body shape in spadefoot toads (Martin and Pfennig, 2009).

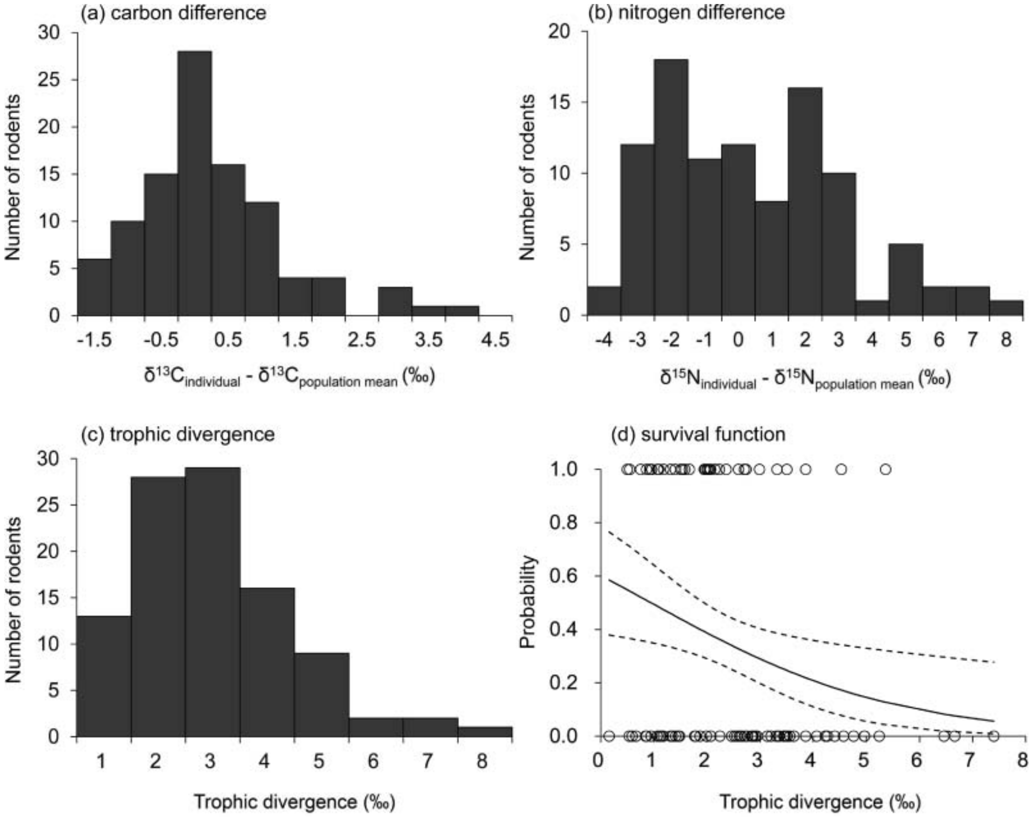

Fig. 5. Frequency distributions of individual differences in trophic niche from the population mean in *Apodemus semotus* and survival as a function of trophic divergence. The individual differences in stable carbon (a) and nitrogen (b) isotope values from the population mean, in units of ‰, are directional. An individual can have positive or negative values depending on whether it has higher or lower isotope values than the population mean. Trophic divergence (c) quantified by Euclidean distance between an individual and the population mean on the $\delta^{13}C$–$\delta^{15}N$ bi-plot, in units of ‰, is non-directional. The solid and dashed lines (d) denote predicted mean survival and its 95% confidence limits based on the equation: logit (survival) = 0.41 ± 0.45 (s.e.) − 0.44 ± 0.18 × trophic divergence. The circles denote actual observations. The same regression lines but with different symbols used for actual observations from different trapping sessions are provided in Fig. S2 (see evolutionary-ecology.com/data/2796Appendix.pdf).

In all of the above cases, however, different morphs are closely matched to distinct diets, such as benthic versus limnetic prey in sticklebacks (Bolnick, 2004). Given that morphology is heritable, a system with close matching between trophic morphology and diet should be particularly subject to rapid evolution. Directional selection is less likely for those species in which diet is largely determined by plastic behaviour instead of heritable morphological traits. Although feeding adaptations in rodents involve morphological changes, trophic morphology (e.g. dental shape) in generalists such as *Apodemus* is extremely conserved over evolutionary time (Renaud *et al.*, 2005). Omnivorous rodents may thus rely more on behavioural plasticity to cope with short-term and fine-scale variation in resource–consumer dynamics while still maintaining a stable trophic niche over time.

Both the need to balance nutrients (e.g. Lewis *et al.*, 2001; Mayntz *et al.*, 2005), and competition from heterospecific trophic specialists (e.g. Martin and Pfennig, 2009), could have contributed to the conserved trophic niche in this population of *A. semotus*. Based on the isotope data of the six repeatedly captured individuals, we suspect that some level of consistency in diets might be necessary for long-lived individuals. Specifically, among these six individuals, individual identity explained 19% and 60% of the variation in δ^{13}C and δ^{15}N values respectively, whereas trapping session explained 27% and 0%. The consistency in diets occurred despite fluctuations in seed and arthropod abundances over time, suggesting that there might be an optimal dietary composition for these rodents. Such an optimum could emerge if the diet of *A. semotus* is constrained by co-existing trophic specialists such as herbivorous voles *Eothenomys melanogaster* and insectivorous shrews *Anourosorex yamashinai*.

Inferences on niche divergence or conservatism are sensitive to the traits or niche axes being considered (Wiens *et al.*, 2010). For example, Darwin's finches show distinct beak size morphs, each specializing on a different type of seed (Hendry *et al.*, 2009). However, they all belong to the granivore niche, and from the perspective of functional groups, their trophic niche is conserved. In contrast, spadefoot toads show distinct omnivore and carnivore morphs, each playing a different functional role in food webs (Martin and Pfennig, 2009). In species where trophic morphs are less likely, stable isotope values, specifically Euclidean distance between an individual and the population mean on the δ^{13}C–δ^{15}N bi-plot, have the potential to be widely applied to studies of niche evolution at the level of organisms' functional role. More generally, this approach does not rely on the matching between trophic morphology and trophic niche, and provides universal niche axes for all consumer species.

ACKNOWLEDGEMENTS

We thank Erik Hobbie for his comments on the analyses, and Jenn-Che Wang for his assistance on plant identification. Two anonymous reviewers provided useful comments on an earlier draft of the manuscript. This work was funded by the National Science Council in Taiwan (NSC 99-2621-B-003-001).

REFERENCES

Ackermann, M. and Doebeli, M. 2004. Evolution of niche width and adaptive diversification. *Evolution*, **58**: 2599–2612.

Bolnick, D.I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, **58**: 608–618.

Bowen, S.H., Lutz, E.V. and Ahlgren, M.O. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, **76**: 899–907.

Claridge, A.W. and May, T.W. 1994. Mycophagy among Australian mammals. *Aust. J. Ecol.*, **19**: 251–275.

Claridge, A.W., Trappe, J.M., Cork, S.J. and Claridge, D.L. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. *J. Comp. Physiol. B.*, **169**: 172–178.

Darimont, C.T., Paquet, P.C. and Reimchen, T.E. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *J. Anim. Ecol.*, **78**: 126–133.

Denno, R.F. and Fagan, W.F. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, **84**: 2522–2531.

Hendry, A.P., Huber, S.K., de León, L.F., Herrel, A. and Podos, J. 2009. Disruptive selection in a bimodal population of Darwin's finches. *Proc. R. Soc. Lond. B.*, **276**: 753–759.

Holt, R.D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. USA*, **106**: 19659–19665.

Holt, R.D. and Gaines, M.S. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.*, **6**: 433–447.

Holt, R.D. and Gomulkiewicz, R. 1997. The evolution of species' niches: a population dynamic perspective. In Case Studies in Mathematical Modeling: Ecology, Physiology and Cell Biology (H.G. Othmer, F.R. Adler, M.A. Lewis and J.C. Dallon, eds.), pp. 25–50. Upper Saddle River, NJ: Prentice Hall.

Huang, B.M., Lin, L.K. and Alexander, P.S. 1997. Annual reproductive cycle of the Formosan wood mouse, *Apodemus semotus. Zool. Stud.*, **36**: 17–25.

Knudsen, R., Klemetsen, A., Amundsen, P.A. and Hermansen, B. 2006. Incipient speciation through niche expansion: an example from the Arctic charr in a subarctic lake. *Proc. R. Soc. Lond. B.*, **273**: 2291–2298.

Lehmkuhl, J.F., Gould, L.E., Cázares, E. and Hosford, D.R. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. *Forest Ecol. Manage.*, **200**: 49–65.

Lewis, C.E., Clark, T.W. and Darting, T.L. 2001. Food selection by the white-footed mouse (*Peromyscus leucopus*) on the basis of energy and protein content. *Can. J. Zool.*, **79**: 562–568.

Lin, L.-K. and Shiraishi, S. 1992. Demography of the Formosan wood mouse *Apodemus semotus*. *J. Faculty Agriculture, Kyushu Univ.*, **36**: 245–266.

MacAvoy, S.E., Macko, S.A. and Arneson, L.S. 2005. Growth versus metabolic tissue replacement in mouse tissues determined by stable carbon and nitrogen isotope analysis. *Can. J. Zool.*, **83**: 631–641.

Mangan, S.A. and Adler, G.H. 2000. Consumption of arbuscular mycorrhizal fungi by terrestrial and arboreal small mammals in a Panamanian cloud forest. *J. Mammal.*, **81**: 563–570.

Martin, R.A. and Pfennig, D.W. 2009. Disruptive selection in natural populations: the roles of ecological specialization and resource competition. *Am. Nat.*, **174**: 268–281.

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. and Simpson, S.J. 2005. Nutrient-specific foraging in invertebrate predators. *Science*, **307**: 111–113.

McCormack, J.E. and Smith, T.B. 2008. Niche expansion leads to small-scale adaptive divergence along an elevation gradient in a medium-sized passerine bird. *Proc. R. Soc. Lond. B.*, **275**: 2155–2164.

Newsome, S.D., del Rio, C.M., Bearhop, S. and Phillips, D.L. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.*, **5**: 429–436.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**: 703–718.

Renaud, S., Michaux, J., Schmidt, D.N., Aguilar, J.P., Mein, P. and Auffray, J.C. 2005. Morphological evolution, ecological diversification and climate change in rodents. *Proc. R. Soc. Lond. B.*, **272**: 609–617.

Roth, J.D. 2002. Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, **133**: 70–77.

Shaner, P.L. and Macko, S.A. 2011. Trophic shifts of a generalist consumer in response to resource pulses. *PLoS One*, **6**: e17970.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*, **10**: 1115–1123.

Stapp, P., Polis, G.A. and Piñero, F.S. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. *Nature*, **401**: 467–469.

Vanderklift, M.A. and Ponsard, S. 2003. Sources of variation in consumer-diet delta ^{15}N enrichment: a meta-analysis. *Oecologia*, **136**: 169–182.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.*, **13**: 1310–1324.

Yu, H.T. 1993. Natural history of small mammals of subtropical montane areas in central Taiwan. *J Zool.*, **231**: 403–422.