Age-related plasticity integration in male cicadas Tettigetta isshikii

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Abstract

Labile traits, such as behavioural, physiological traits or body mass, exhibit variation within an individual either over time or across environments. Such changes within an individual can be linked across traits, forming within-individual trait correlations. These correlations are particularly expected when ageing causes changes in the expression of multiple traits. The direction of these correlations also depends on mechanisms explaining age-related changes in each traits, such as physiological deterioration or changes in future fitness expectations. Therefore, assessing within-individual trait correlations offers insights into the trait-specific ageing patterns, their integration and age-related reproductive strategies. Here, we tracked individual male cicadas (Tettigetta isshikii) in their natural habitat, repeatedly assessing their plant use (narrow vs. wide-leafed), calling activity, and body mass. Results revealed that male cicadas lost mass, increased calling activity and a preference for narrow-leafed plants as they aged. This integration of age-related plasticity led to negative within-individual correlations between body mass and behaviours. The asset protection principle could explain the age-related increase in calling activity and the preference for narrow-leafed plants. Such an age-related increase in energetically demanding calling activity may also cause an age-related decrease in body mass. Considering that adult cicadas consume nutritionally poor xylem sap, the negative within-individual correlations between body mass and risk-taking behaviour suggest that T. isshikii males follow a capital breeding strategy rather than an income breeding strategy. Therefore, we emphasise the importance of individual-level tracking study in the wild to achieve a comprehensive understanding of the life-history strategies and behavioural ecology of a study animal.

Age-related plasticity integration in male cicadas *Tettigetta isshikii*

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Author Contribution Statement

JH - Conceptualization; Data curation; Investigation; Visualization; Roles/Writing – original draft; Writing – review & editing.

CSH - Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Supervision; Roles/Writing – original draft; Writing – review & editing.

Abstract

Labile traits, such as behavioural, physiological traits or body mass, exhibit variation within an individual either over time or across environments. Such changes within an individual can be linked across traits, forming within-individual trait correlations. These correlations are particularly expected when ageing causes changes in the expression of multiple traits. The direction of these correlations also depends on mechanisms explaining age-related changes in each traits, such as physiological deterioration or changes in future fitness expectations. Therefore, assessing within-individual trait correlations offers insights into the trait-specific ageing patterns, their integration and age-related reproductive strategies. Here, we tracked individual male cicadas (*Tettigetta isshikii*) in their natural habitat, repeatedly assessing their plant use (narrow vs. wide-leafed), calling activity, and body mass. Results revealed that male cicadas lost mass, increased calling activity and a preference for narrow-leafed plants as they aged. This integration of age-related plasticity led to negative within-individual correlations between body mass and behaviours. The asset protection principle could explain the age-related increase in calling activity and the preference for narrow-leafed plants. Such an age-related increase in energetically demanding calling activity may also cause an age-related decrease in body mass. Considering that adult cicadas consume nutritionally poor xylem sap, the negative within-individual correlations between body mass and risk-taking behaviour suggest that *T. isshikii* males follow a capital breeding strategy rather than an income breeding strategy. Therefore, we emphasise the importance of individual-level tracking study in the wild to achieve a comprehensive understanding of the life-history strategies and behavioural ecology of a study animal.

Keywords: cicada, *Tettigetta isshikii* , within-individual variation, within-individual correlation, ageing, plasticity, capital breeding

Introduction

Within an individual, the expression of labile traits (e.g., behavioural, physiological or morphological traits such as body mass) can exhibit variation with individuals adjusting their phenotypes over time or in response to environmental changes. Moreover, within-individual plastic changes in multiple traits can also be associated across traits (Dingemanse et al. 2012; Dingemanse and Dochtermann 2013). If the expression of multiple traits is based on a shared underlying mechanism or these traits affect each other via a feedback loop (Sih et al. 2015), we would expect to find an association between within-individual changes in multiple traits. For instance, if exercise elevates the plasma level of corticosterone in mice (Girard et al. 2002), the daily pattern of exercise is expected to align with that of corticosterone levels. In addition, as a high metabolic rate is needed to express energetically demanding behaviour (such as risk-taking behaviour)**, within-individual changes in the** resting metabolic rate are expected to parallel those in risk-taking behaviour (e.g, Cornwell et al. 2020). **The correlation between changes in multiple traits within an individual is termed a "within-individual trait correlation" (Dingemanse and Dochtermann 2013). Multiple traits may change (or fluctuate) in the same direction within an individual, causing a positive within-individual trait correlation (scenarios 1 and 3 in Figure 1). Conversely, traits may change (or fluctuate) in opposite directions within an individual, causing a negative within-individual trait correlation (scenarios 2 and 4 in Figure 1).**

Within-individual trait correlations are strongly expected when trait expression is dependent on age (scenarios 1 and 2 in Figure 1). Notably, since individual differences in behaviour can stem from variations in state variables **(Biro and Stamps 2008; Dingemanse and Wolf 2010; Wolf and Weissing 2010; Sih et al. 2015), age-related decreases in labile state variables (e.g., body mass, metabolic rate and hormone levels) are expected to** correspond with **decreases in behaviours, leading to positive within-individual correlations between state variables and behaviours (scenario 1 in Figure 1). In this scenario,** physiological deterioration with ageing may diminish state trait levels, subsequently reducing the expression of state-dependent behavioural traits and resulting in a positive within-individual correlation between state and behaviour**. For example,** in male field crickets *Gryllus campestris* , both body mass and exploration decrease with age, leading to a positive within-individual correlation between body mass and exploration (Santostefano et al. 2016). In addition to ageing, there may be a positive feedback loop between body mass and exploration in the field cricket (e.g., reduced body mass decreases exploration, and vice versa), further contributing to a positive within-individual correlation between body mass and exploration.

In addition, **within-individual trait correlation can be an outcome of age-related changes in future fitness expectations (i.e., residual reproductive value, Williams 1966). According to the asset protection principle (Clark 1994), individuals tend to take more risks when their future fitness expectation is low, and when the reproductive costs from injury or death are less important (Clark 1994; Luttbeg 2017). Consequently, older individuals with lower expected future fitness are more likely to exhibit risk-taking behaviour (e.g., Dammhahn 2012; Fisher et al. 2015; Ory et al. 2015; Moschilla et al. 2018), potentially resulting in strongly positive within-individual correlations among risk-taking behaviours. Moreover, if age-related decreases in state variables such as body mass reflect changes in future fitness expectations (e.g., body mass determines dominance), a decrease in body mass with age would be integrated with the age-related increase in multiple risk-taking behaviours, resulting in a negative within-individual correlation between body mass and risk-taking behaviour (scenario 2 in Figure 1).**

Overall, the direction of within-individual trait correlations between state and behaviour can vary depending on the trait-specific mechanisms leading to age-related increase/decrease or fluctuation (Figure 1). Recent meta-analyses have indicated a weak relationship between state and behaviour at both the within-individual and among-individual levels (Niemelä and Dingemanse 2018); however, this might be attributed to a paucity of studies conducting frequent repeated measurements of labile traits with longer intervals between repeated measures. Therefore, it is imperative to assess within-individual trait correlations to identify the underlying trait-specific or common mechanisms shaping age-related plasticity. However, within-individual correlations have garnered considerably less attention from behavioural ecologists (Dochtermann 2023).

In this study, we tracked individual male cicadas *Tettigetta isshikii* (Figure 2) in their natural habitat and repeatedly assessed their plant use, calling activity, and body mass. We investigated age-related changes in these traits, partitioned trait variance into among- and within-individual levels, and estimated among- and within-individual correlations among these traits. In this study, we predicted that two behaviours, plant use and calling activity, would reflect the boldness of each male. Cicadas actively use plants as shelters, adjusting their location within the plant to hide themselves (Steward et al. 1988). Different plant species vary in structural characteristics, such as leaf size and density, suggesting the shelter they provide for cicadas may differ by species. Cicadas might prefer plants with larger, denser leaves to protect them from aerial predators (e.g., robber fly). *T. isshikii* also feeds on herbaceous plant sap and lays its eggs in plant stems, potentially using the plants as shelters by hiding underneath the leaves (Jiman Heo, personal observation). In our study area, plants such as *Erigeron annuus* (Daisy fleabane)*, Thalictrum aquilegiifolium* (Meadow rue), or*Miscanthus sinensis* (Chinese silver grass) have narrow or small leaves, whereas only 2 plants, *Convallaria majalis* (Lily of the valley) and *Polygonatum odoratum* (Solomon's seal), have large leaves and occurs in discrete clusters (Figure 3). As a result, only*C. majalis* and *P. odoratum* may effectively function as a shelter for *T. isshikii.* Thus, we predicted that the increased use of narrow-leafed plants might indicate greater boldness in the face of potential predators. In addition, male *T. isshikii* produces calls to attract females, and females respond with wing-flicking sounds (Jiman Heo, personal observation). However, calling songs of cicadas increases predation risk by predators such as the robber fly (Hou et al. 2017), suggesting that calling can also be considered a risk-taking behaviour of male *T. isshikii* .

We predicted that trait-specific mechanisms shaping age-related plasticity would determine within-individual trait correlations. If physiological deterioration leads to both reductions in calling activity and boldness with age as well as weight loss in male cicadas after eclosion and maturation, positive within-individual correlations between body mass and risk-taking behaviours are expected (scenario 1 in Figure 1). In contrast, according to the asset protection principle, male cicadas might increase the expression of risk-taking behaviours with age, even as body mass decreases (scenario 2 in Figure 1). This scenario could lead to negative within-individual correlations between body mass and risk-taking behaviours. Consequently, we predicted that the integration of age-related plasticity in multiple traits of male cicadas would hinge on the trait-specific mechanisms governing age-related changes.

Materials and Methods

Study species

Tettigetta isshikii (Hemiptera: Cicadettinae) is a small cicada species distributed across East Asia, including Korea, Russia (Sakhalin, Ussuri, and Siberia), and China (Lee 2008) (Figure 2A). In Korea, *T. isshikii* is widespread on the mainland but not on the small islands, except for Jeju Island (Lee 2008). The species is found at various altitudes, ranging from 30 metres to as high as 1,000 metres (Lee et al. 2004; Jiman Heo, personal observation). Since *T. isshikii* adults feed on xylem sap from herbaceous plants and lay eggs in the stem of herbaceous plants, they are rarely found on trees (Jiman Heo, personal observation). During the day, adult male *T. isshikii* produce long calls to attract females, but they remain silent at night (Lee et al. 2004; Jiman Heo, personal observation).

Study site

The field observation was carried out in a grassfield located in PyeongChang-gun, Gangwon-do, Korea (37°34'53.9"N 128°24'58.6"E, altitude: 590 m). The site was a rectangular grassy field (area: 30×8 m = 240 m^2) containing diverse herbaceous plants. The field was enclosed by oak and pine trees, and cicadas were exclusively observed within this area. Throughout the observations, we measured temperature and humidity using a thermometer and humidity meter (Testo 174H Mini data logger, Germany). Notably, the temperature and humidity variations during the three observation periods (detailed below) within a day corresponded closely to the observation time (i.e., temperature always increased but humidity decreased from morning to mid-afternoon observation period) (Figure S1). As a result, temperature and humidity were excluded from the subsequent analysis.

Field observations and morphological measurements

Observations were conducted three times per day (from 09:00 to 10:00, 12:00 to 13:00, and 15:00 to 16:00) between June 1st and June 13th, 2022, excluding June 6th due to rain. Consequently, the maximum count of daily observations for each individual was three or fewer. During the observation periods, as the observer walked through the habitat, whenever we found individuals, we captured them using a net, weighed them using a scale (Pocket Scale MH-100) to the nearest 0.01 g, and subsequently released them at their original location. Previously unmarked (newly found) individuals were individually marked with on their left wing with a paint marker (PC–3M, POSCA) to render them individually identifiable (Figure 2B).

When we found cicadas, we also recorded plant species on which the individuals were located. In the study area, cicadas were found on multiple herbaceous plants such as *Convallaria majalis* (Lily of the Valley), *Polygonatum odoratum* var. *pluriflorum* (Solomon's seal), *Miscanthus sinensis* (Chinese silver grass),*Erigeron annuus* (Daisy fleabane), *Cirsium japonicum* (Japanese thistle), and *Thalictrum aquilegiifolium* var.*sibiricum* (Meadow rue) (Figure 3). Among the plants, only*C. majalis* and *P. odoratum* have large leaves, and we predicted that these two species can effectively function as a shelter for *T. isshikii* . Thus, in the analysis of individual plant use, we focused on whether the cicadas were found in large-leafed (*C. majalis* and *P. odoratum*) or small- and narrow-leafed plants (other plant species).

During the observation, we also recorded whether males produced calls or not. *Tettigetta isshikii* males consistently produced calling regardless of the presence of a quietly walking observer (Jiman Heo, personal observation). Males were assigned a score of 1 when engaged in calling and a score of 0 when silent.

Although we marked 41 males and 23 females in the field, we failed to sample a sufficient number of female individuals and lacked sufficient observations to conduct variance partitioning analyses. Thus, in this study, we focused on the analyses of data collected from males. We collected 103 behavioural and morphological samples from males, and repeated measurements were taken 2.45 on average per individual.

Statistical analyses

Our first set of analyses using univariate mixed-effects models examined individual differences in trait expression and how trait expression changed with age or time within a day. Our second set of analyses using bivariate mixed-effect models estimated within-sex among- and within-individual correlations between traits.

Univariate models. The univariate models fitted individual identity as a random effect and (within-individual mean-centred) observation day and (mean-centred) time of day as covariates. We used the following error structure for the response variable: body mass was modelled with Gaussian errors, plant use (found in narrow-leafed plants (1) or not (0)) and calling activity (exhibiting calling (1) or not (0)) were modelled with binomial errors. Despite including a quadratic term of observation day (i.e., age) as an additional covariate in the univariate models, we did not observe quadratic ageing patterns in any of the traits (results not included). Consequently, the univariate models did not include a quadratic term of observation day. In addition to the random intercept model, we used a random slope model to estimate among-individual variation in age-related plasticity. We found no variation in the age-related slopes (results not included).

All univariate mixed-effects models were implemented in ASReml (version 4.1, VSN Interaction, Hemel Hempstead, UK) and solved using the restricted maximum likelihood method. *The significance of fixed effects was assessed through conditional Wald F tests. Statistical significance for variance was determined using a likelihood-ratio test (LRT). To examine deviations from zero variances, LRTs were conducted, involving the difference in deviance (-2 × log likelihood) between the full model and a model* where the variance was removed*. The P value was computed under the assumption of an equal combination of* P (χ^2, df = 0) and P(χ^2, df = 1) (hereafter, $\chi^2{}_{0/1}$).

Bivariate models. We constructed sets of bivariate models, where we fitted two traits from plant use, calling activity, and body mass as the response variables. These models included individual identity as a random effect and had no fixed effects. In the bivariate models, we constrained the among-individual covariance between plant use and other traits to zero because the among-individual variance in plant use was not significantly positive (see Results). The within-individual variances in plant use and calling activity were fixed to one because they were not estimable with binary data. Thus we were not able to calculate a within-individual covariance between calling activity and plant use. We fitted the bivariate models within a Bayesian framework using the MCMCglmm package (Hadfield 2010) in R (version 3.2.0). To minimise autocorrelation among samples, 1,300,000 Markov Chain Monte Carlo (MCMC) iterations were performed, which were sampled at 1,000-iteration intervals after an initial burn-in period of 300,000 iterations, using Gamma priors. This resulted in a total of 1000 samples from the posterior distribution. Convergence was attained by visual inspection of output plots and by ensuring that autocorrelation between consecutive samples did not exceed 0.1 (Hadfield 2010).

Results

Cicadas significantly varied in their body mass and calling activity but not in their use of the narrow-leafed plant*s* (Table 1). Body mass and calling activity were not associated at the individual level (Table 2). Behaviours were not function of time of day (Time of day effect, Table 1). However, with repeated observations, cicadas lost body mass, were found in narrow-leafed plant species and increased calling activity (Age effect, Table 1). These age-related plasticities were reflected in within-individual trait covariations: 95% CI of within-individual covariations between body mass and behaviours were smaller than zero (Table 2).

Discussion

We demonstrated that male cicadas lost body mass, increased calling activity and moved to open habitats (narrow-leafed plants) with age. Such integration of age-related plasticity resulted in negative within-individual covariations between states (body mass) and risk-taking behaviours. This pattern may be attributed to the combined effects of asset protection and energetically demanding mate calling. The age-related decrease in body mass might be due to age-related increase in calling efforts, and the age-related increase in risk-taking behaviours might be due to decreased future fitness expectations with age. Moreover, the integration of age-related plasticity in *T. isshikii* implies that *T. isshikii* exhibits a capital breeding reproductive strategy.

Considering the age-related increase in calling activity, physiological deterioration may not occur in wild cicadas, although this remains uncertain. This age-related increase in calling activity might be due to the immaturity of younger males, who are not yet capable of producing calls. However, a quadratic ageing pattern was not evident in male calling activity, as the increased calling activity did not decline with age. This suggests that the changes in calling activity are not due to physiological deterioration. Nevertheless, the possibility of physiological deterioration cannot be entirely dismissed. Despite thorough searches of the habitat, it is possible that non-calling older males were missed, potentially biasing the analysis of age-related changes in calling activity. For instance, a non-linear ageing pattern in calling behaviour might exist, but our study could fail to detect it if non-singing old males were overlooked during our observations.

The age-related increase in risk-taking behaviour among male *T. isshikii* can be explained by the asset protection principle (Clark 1994). In the analysis of plant use, males were found in narrow or small-leafed plant species with age. Considering that plants provide shelters, *T. isshikii* may safely hide in large-leafed plants when they were young adults. As male cicadas age, they may prefer staying in narrow-leafed plants to increase body temperature and calling activity, actively advertising their locations to females. Therefore, following the asset protection principle, male cicadas stay in large-leafed plants to maximise protection with no courtship activity during early adulthood, while they move to narrow-leafed plants and actively seek mates during late adulthood. These behavioural strategies likely maximise the reproductive success of male cicadas during their short reproductive periods.

The age-related decrease in body mass among cicadas might be attributed to the stress from repeated net captures as well as the age-related increase in the energetically demanding calling activity. Although we minimised disturbance by quickly confirming their identity before release, the repeated netting could still potentially contribute to a decline in body mass over time. Moreover, if the stress from repeated captures and the principle of asset protection are both active, this stress could reduce body mass and subsequently lead to increased risk-taking behaviours. Therefore, we cannot completely rule out the possibility that our collecting methods may influence the ageing process of cicadas, potentially affecting the within-individual correlations between body mass and risk-taking behaviours.

Instead of the role of stress in shaping within-individual correlations between body mass and risk-taking behaviours, the age-related decrease in body mass and increase in risk-taking behaviour in male cicadas may imply the resource allocation strategies for reproduction. There are two extreme resource allocation strategies according to the timing of reproduction: capital breeding and income breeding (Jönsson and Jonsson 1997; Drent and Daan 1980). Capital breeders accumulate resources before the reproductive period and utilise them during reproduction, while income breeders depend on current resource acquisition during reproduction (Jönsson and Jonsson 1997). Considering the continuum from pure capital breeding to pure income breeding, many insect species lean towards being income breeders. Although larval nutritional conditions influence adult phenotypes and life history (reviewed in Scriber and Slansky 1981; Awmack and Leather 2002; Han and Dingemanse 2015; Koyama and Mirth 2018), many insects consume macronutrients during the reproductive period and use resources acquired during the adult stage directly for reproduction (i.e., income breeders). Some insect species are recognised as capital breeders (Tammaru and Haukioja 1996; Boggs 1997; Kemp and Alcock 2003; Casas et al. 2005; Johnson 2006; Bauerfeind and Fischer 2008; Rhainds et al. 2008; Pöykkö 2009; Davis et al. 2016), but cicadas have not been extensively studied in this context.

Cicadas do not strictly adhere to a pure capital breeding strategy because they are known to consume a substantial amount of xylem sap as adults (Cheung and Marshall 1973). Both nymph and adult cicadas feed on xylem (Brown and Chippendale 1973; Cheung and Marshall 1973; WHITE and STREHL 1978), which contains mainly water (99%) but includes nutrients such as carbohydrates, amino acids, and proteins at very low concentrations (Satoh et al. 1992; Dafoe and Constabel 2009). Water intake may be the primary aim of adult cicada's intake of xylem sap because the water loss across the cuticle is high in cicada (Hepler et al. 2023). Instead, in cicadas, the nutrient necessary for reproduction may be collected during nymphal stage. Both nymphs and adults rely on nutritionally poor xylem sap for nutrient intake (Cheung and Marshall 1973; WHITE and STREHL 1978). However, as the nymphal stage is much longer compared to adult stage, nymphs can have enough time to accumulate reserves and grow (White and Lloyd 1975). Thus, adult cicadas seem to rely on resources stored during the larval stage for reproduction. Actually, female cicada fecundity is also known to depend on resource acquisition during the larval stage (Brown and Chippendale 1973). Therefore, we suggest that the capital breeding strategy is more prominent in *T. isshikii* . To further evaluate whether resource allocation strategies during cicada reproduction are more aligned with those of capital breeders along the income-capital breeding continuum, future studies should investigate how food intake during nymph and adult stages affects reproductive output.

Alternatively, if body mass influences agility in escaping predators in cicadas, this can also lead to within-individual correlations between body mass and risk-taking behaviours. In flying insect species, heavier body mass has been shown to reduce individual agility in escaping predators, increasing predation risk (McLachlan et al. 2003; Roitberg et al. 2003). Although the relationship between predation rate and body mass has not been assessed in cicada species, poor agility caused by heavy body mass during early adulthood may make calling males more vulnerable to predators such as robber flies. Therefore, it might be advantageous for young males to reduce their calling activity and move cautiously. However, as body mass decreases with age, increased agility in escaping predators can reduce the predation risk of older males. This may enable older males to be more active in finding mates and producing calls. Thus, the relationship between body mass and predation risk may explain within-individual correlations between body mass and risk-taking behaviours in our study. However, if body mass affected predation risk in cicadas, a negative among-individual correlation would also be expected between risk-taking behaviours and body mass, but we found no such correlation. Therefore, we suggest that within-individual trait correlations in *T. isshikii* are not explained by a relationship between body mass and predation risk.

While individual-level behavioural studies with repeated measures experimental design have been extensively conducted across various animal taxa in the wild (as reviewed in Hertel et al. 2020), such investigations are less common in insects (but see Fisher, David, et al. 2015; Fisher, James, et al. 2015; Niemelä et al. 2015; Golab et al. 2021; Niemelä et al. 2021). This scarcity might arise from the challenges of distinguishing and tracking individual insects in their natural habitats. Despite a recent study demonstrating the existence of personality traits in cicadas under laboratory conditions (Roth et al. 2022), no studies have tracked individual cicadas in the wild, repeatedly measured their behaviour, and assessed individual differences. Our field study addressed this gap, providing insights into the behavioural ecology of cicadas, specifically shedding light on the reproductive and life history strategies of *T. isshikii* males. Our study revealed the integration of age-related plasticity in body mass and risk-taking behaviours, resulting in within-individual correlations among these traits in male cicadas. The asset protection principle could explain the age-related increase in calling activity and the preference for narrow-leafed plants. Such an age-related increase in energetically demanding behaviour may also cause an age-related decrease in body mass. While adult cicadas rely on nutritionally poor xylem sap, the age-related decrease in body mass was associated with an age-related increase in risk-taking behaviour, suggesting that *T. isshikii* males resemble capital breeders more than income breeders. Thus, we emphasise that studying individual behaviour in the wild is crucial to achieve a comprehensive understanding of the behavioural ecology of the study animal and the evolutionary processes that shape their behaviours and life-history strategies in the wild.

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Tables

Table 1. Age-related plasticity and individual differences in plant use, calling activity and body mass of male cicadas. Parameters are provided with standard errors (SE) in parentheses.

	Plant use [a]		**Calling activity**	**Body mass**			
Fixed effects	β (SE)	$F_{NUMdf,DENdf}$	P	β (SE)	$F_{NUMdf,DENdf}$	P	β (SE)
Intercept	-0.43 (0.25)	$2.83_{1,32.8}$	0.10	0.11 (0.27)	$0.18_{1,30.1}$	0.68	0.12 (0
Time of day [b]	**0.49 (0.33)**	**$2.29_{1,91.0}$**	**0.13**	**0.07 (0.31)**	**$0.05_{1,100.0}$**	**0.82**	
Age [c]	**0.34 (0.17)**	**$4.21_{1,91.0}$**	**0.04**	**0.30 (0.15)**	**$4.00_{1,100.0}$**	**0.04**	**-0.22**
Random effects	σ^2 (SE)	χ^2_{df}	P	σ^2 (SE)	χ^2_{df}	P	σ^2 (SE

	Plant use [a]		**Calling activity**	**Body mass**			
ID	0.46 (0.50)	$1.23_{0/1}$	0.13	0.87 (0.63)	$7.45_{0/1}$	0.003	0.51 (0
Residual	1.00 (-)			1.00 (-)			0.43 (0

[a] **The tendency to be found in narrow-leafed plants**

[b] **Within-group centred time of day (-1=09:00 to 10:00, 0=12:00 to 13:00, and 1=15:00 to 16:00)**

[c] **Within-individual mean-centred testing day**

Table 2. Among- and within-individual trait covariances.

Among-individual level	Covariance (95% confidence interval)
Body mass – Calling activity	-0.38 (-1.15, 0.26)
Body mass – Plant use [a]	NA [b]
Plant use – Calling activity	NA [b]
Within-individual level	Covariance (95% confidence interval)
Body mass – Calling activity	-0.42 (-0.74, -0.04)
Body mass – Plant use [a]	-0.40 (-0.78, -0.07)
Plant use – Calling activity	NA

[a] **The tendency to be found in narrow-leafed plants**

[b] **The among-individual covariances between plant use and other traits were not able to be calculated due to the absence of among-individual variance in plant use.**

Figures

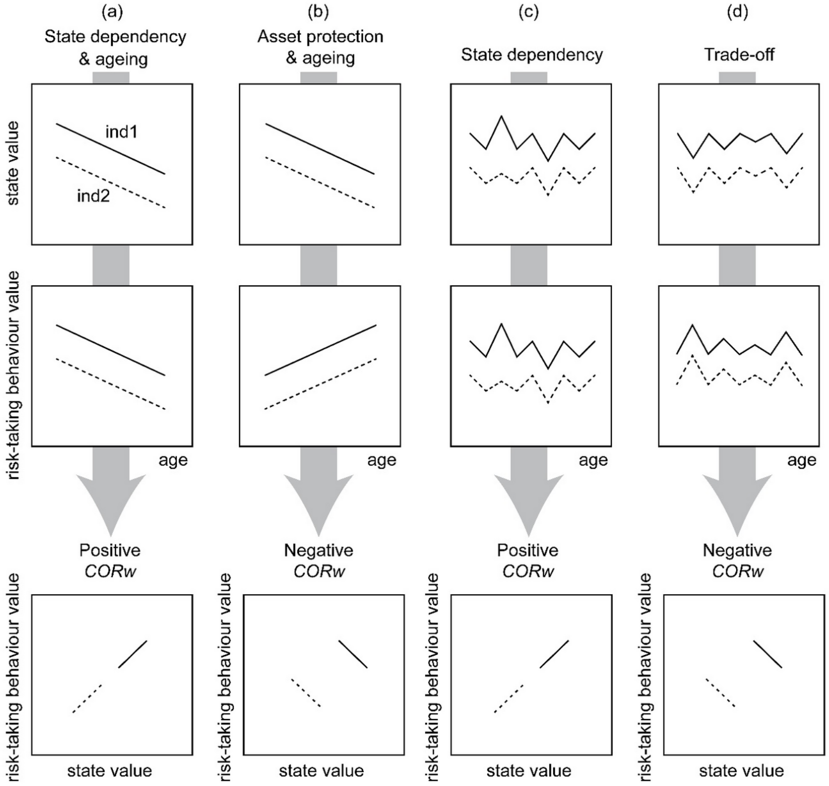

Figure 1. Hypothetical scenarios shaping within-individual correlations (*CORw*) between state and risk-taking behaviour. Temporal changes in traits, specifically related to ageing, strongly shape within-individual trait correlations (a,b). (a) A positive within-individual trait correlation is expected when both individual state and behaviours decline with age due to physiological deterioration. (b) A negative within-individual trait correlation is expected when individuals are more likely to engage in risk-taking behaviour with decreasing future fitness expectations with age. However, within-individual trait correlations can occur even when traits do not change with age, but fluctuate based on (c) state dependence or (d) trade-off.

Figure 2. (A) A *Tettigetta isshikii* individual resting on a *Convallaria majalis* leaf. *(B)* A *T. isshikii*individually marked on their wings using enamel paints. (Photo credit: Jiman Heo)

Figure 3. Plant species on which cicadas *Tettigetta isshikii were found in their natural habitat. Large-leafed plants: (A) Convallaria majalis* and (B) *Polygonatum odoratum* var.*pluriflorum*; Narrow-leafed plants: (C) *Miscanthus sinensis*, (D) *Erigeron annuus*, (E) *Cirsium japonicum*, and (F) *Ixeridium dentatum* **(Photo credit: Jiman Heo, Myeong Dong Cho)**