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Trait compensation between boldness and the propensity for tail autotomy under different food availabilities in similarly aged brown anole lizards

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Summary

1. Trait compensation denotes the situation in which individuals offset the costs of one trait with the benefits of another trait. The phenomenon of trait compensation is best exemplified by a negative correlation between the degree of predator avoidance and the strength of morphological defence.

2. In this study, we used the relationship between risk-taking tendency (boldness) and the propensity for tail autotomy in the brown anole lizards *Anolis sagrei* to address two important questions regarding trait compensation. First, we investigated whether trait compensation existed among individuals of similar age. Second, we examined how the relationship between boldness and the propensity for tail autotomy responded to changes in food availability.

3. Overall, bolder individuals autotomized their tails more readily. Although mean values of boldness and the propensity for tail autotomy did not differ under high and low food availability, the compensatory effect between the two traits was only obvious when food was abundant.

4. The existence of trait compensation among similarly aged individuals will serve as the first step to understanding the evolution of compensatory effects among traits observed at higher level. In addition, food availability affected the dynamics of trait compensation by influencing the amount of variation of traits involved, rather than altering the mean values of traits *per se*.

Key-words: animal personality, behavioural defence, diet, growth, morphological defence

Introduction

Trait compensation describes how individuals can offset the costs of one trait with the benefits of another trait (DeWitt, Sih & Hucko 1999). Such a compensatory effect is increasingly recognized as underlying the evolutionary trajectories of suites of fitness-related traits (Husak & Swallow 2011; Dennenmoser & Christy 2013; Lailvaux, Wilson & Kasumovic 2014). The phenomenon of trait compensation is best exemplified by the relationship between morphological and behavioural defence traits, in which morphologically more vulnerable individuals tend to display higher degrees of predator avoidance and vice versa (e.g. Rundle & Bronmark 2001; Cotton, Rundle & Smith 2004; Mikolajewski 2004). However, the degree of predator avoidance is often a manifestation of an individual's intrinsic risk-taking tendency or 'bold-shy' personality (Gosling 2001; Sih *et al.* 2004b). Bolder individuals are characterized by their willingness to explore unfamiliar environments, although this behavioural tendency tends to expose those individuals to higher predation risk (Dingemanse & Reale 2005). The existence of trait compensation suggests that bolder individuals may compensate for their risk-taking personality with more effective morphological defence.

Despite substantial amounts of research effort towards understanding trait compensation, two important questions still have not been fully addressed. The first question is how trait compensation originates below the species level. Existing studies examining trait compensation within a species typically compare individuals that differ in body size, in which smaller, morphologically more defenceless individuals tend to be more predator-averse and vice versa (e.g. Rundle & Bronmark 2001). However, in those studies, the variation in body size was not independent of (and likely due to) age, with smaller individuals also likely being younger. While those results provided valuable information on how the relationship between behavioural and

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*Correspondence author. E-mail: chiyun@bio.umass.edu morphological defences changes as individuals grow, they only offered limited insight into how trait compensation might evolve from within a species to higher levels, as doing so would first and foremost require the existence of trait compensation among same-aged individuals. Even though variation in both boldness and morphological defence has been well documented among same-aged individuals (Harvell 1990; Sih, Bell & Johnson 2004a), only a handful of studies have examined trait compensation while taking age difference into account, and none of them detected an unequivocal pattern (Quinn & Cresswell 2005; Lacasse & Aubin-Horth 2012).

The second unanswered question is how trait compensation might respond to changes in resource availability, especially food. Food availability can affect the costs and benefits associated with the expression of various traits, including defence traits. For example, when food levels are low, investing in morphological defence might become more costly, and individuals might consequently benefit more from risky behaviour that enables them to search for new food sources (Steiner & Pfeiffer 2007). The relative investment between morphological defence and risk-taking behaviour therefore could shift according to food availability, which can change the manner in which trait compensation happens. Indeed, existing theories have predicted that the optimal investment in morphological vs. behavioural defence should be finely tuned to food availability (Steiner & Pfeiffer 2007; Higginson & Ruxton 2009; Dingemanse & Wolf 2010). To our knowledge, however, no study has explicitly examined the dynamics of compensation effects between behavioural and morphological defences under different food availabilities.

An excellent system for addressing these issues involves the voluntary shedding of the tail in lizards (tail autotomy, McVean 1975; Bateman & Fleming 2009). Tail autotomy is a costly, close-range escape strategy that normally occurs when a predator makes physical contact with the tail in the attempt to capture the lizard. A series of muscle contractions will then take place at one to three tail vertebrae anterior to the point of stimulus (Arnold 1984), generating a force that splits the vertebra along a transverse plane of structural weakness (i.e. fracture plane), thus separating the tail from the rest of the body. All tail vertebrae, except for the few that are closest to the cloaca, have fracture planes. Tail autotomy can therefore take place almost along the entire length of the tail. In addition, the detached tail makes fast, rhythmic swinging movements for up to 30 min, thereby diverting the attention of the predator away from the escaping lizard (Pafilis, Valakos & Foufopoulos 2005; Higham & Russell 2010). Although tail autotomy involves a reflex process, several lines of evidence indicate that the propensity for tail autotomy is also under conscious control based on the lizard's perception of immediate danger (Arnold 1984; Clause & Capaldi 2006).

Despite its ecological utility, tail autotomy can impose various costs, including increased metabolic demand for regeneration, lower social status, reduced mating success and impaired locomotor performance (reviewed in Bateman & Fleming 2009), although those costs will decrease and eventually disappear as the tail grows back (which may take several months; Cox 1969). The regenerated vertebrae, however, lack fracture planes and cannot be points of future detachment. Therefore, after multiple incidences of autotomy, the tail of a lizard will eventually comprise entirely regenerated vertebrae and cannot be autotomized again (Bateman & Fleming 2009).

Severe fitness consequences following tail autotomy imply that the propensity to discard the tail should be sensitive to changes in the cost-benefit dynamics. Moreover, the fact that tail autotomy is a commonly employed defence trait suggests that bolder individuals might compensate for the resulting higher predation risk by discarding the tail more readily. Using the brown anole lizard *Anolis sagrei*, we tested the following two hypotheses. First, trait compensation exists between boldness and the propensity for tail autotomy among similarly aged *A. sagrei* individuals, and we predicted that bolder individuals will have higher propensities for tail autotomy. Second, reducing food availability will change the relationship between boldness and the propensity for tail autotomy, although the direction of change would depend on the relative costs of the two traits involved and may not be straightforward to predict *a priori*.

Materials and methods

STUDY SPECIES AND STUDY SITE

The brown anole lizard *A. sagrei* is a small-sized lizard native to Cuba and the Bahamas but has become widely invasive in southern North America, where they can achieve high local abundance (Losos, Marks & Schoener 1993). In October 2013, we captured 59 juvenile *A. sagrei* with original tails from one single population in the New Orleans City Park by hand or with a noose. We used a snout-to-vent length (SVL) threshold of 39 mm – the minimum size of adult males (Lee *et al.* 1989) – to select for juveniles. We determined whether a tail is original by its morphology; regenerated tails tended to be shorter, darker in colour and with a blunter tip. We raised all 59 individuals in the laboratory at the University of New Orleans for 3 months (October 2013–January 2014) until they reached sexual maturity and collected data from those that turned out to be male. By doing so, we minimized the potential confounding effect of sex and previous experiences with predators on boldness and the propensity for tail autotomy (e.g. McDermott *et al.* 2013; Toscano, Gatto & Griffen 2013). More importantly, this approach ensured that all individuals in our study belonged to the same ontogenetic stage.

HUSBANDRY AND DIETARY TREATMENTS

We housed *A. sagrei* lizards in individual plastic cages (30 × 16 × 16 cm) with cypress mulch and a perch (30 × 0·5 cm) in an environment of 12 L:12 D light cycle and a constant temperature of 30 °C. The sides of the cages were painted (except at the front) to prevent the lizards from seeing and interacting with one another. We sprayed the lizards with water and provided them with crickets of suitable size supplemented with calcium powder (Fluker's Farms, Port Allen, LA, USA) three times a week from

October 2013 to January 2014. To test the effect of food availability on the dynamics of trait compensation, we randomly assigned individuals to two dietary treatment groups. The first group received one cricket on each feeding day [restricted diet, $n = 29$, SVL (mean ± SD) in October 2013 = 30·48 ± 5·08 mm]; the second group received three crickets per feeding day [unrestricted diet, $n = 30$, SVL (mean ± SD) in October 2013 = 30·00 ± 5·26 mm]. The number of crickets in each dietary treatment was based on previous studies in *A. sagrei* and a congeneric lizard *Anolis carolinensis*, where the restricted diet had significantly limited growth and the development of bite force in juveniles (Lailvaux, Gilbert & Edwards 2012). We were therefore confident that the restricted diet in our study represented an energetically challenging situation and that the difference in food resource level between the two groups was not trivial (see also The Effectiveness of Dietary Treatments in Results).

PERSONALITY TRIALS

In January 2014, we examined boldness in 32 males by observing their exploratory behaviour in a new environment. To confirm the consistence of risk-taking tendency (i.e. the existence of bold-shy personality), we performed two trials on each individual, with an interval of 3 days between trials. This design is widely used to quantify boldness and its short-term repeatability in various taxa (e.g. Quinn & Cresswell 2005; Bell & Sih 2007; Le Galliard *et al.* 2012; DiRienzo, Pruitt & Hedrick 2013). We performed personality trials in a terrarium (90 × 30 × 45 cm), with an opaque separation initially dividing the space into two chambers (15 or 75 × 30 × 45 cm). The smaller space served as the acclimation chamber, and the bigger space represented the new environment harbouring five available perches (30 × 0·5 cm) for lizards to rest on and explore. Before each trial, we placed a lizard into the acclimation chamber along with the perch from its home cage. We allowed the lizard to rest for 20 min before carefully removing the separation and then gave it 40 min to explore the new environment. We sprayed the perches in the new environment with water and dried them between trials to eliminate the scent left by the previous lizard. Behaviour from each trial was recorded with a video camera 1 m above the terrarium. From each video, we recorded the following three variables that captured the boldness of an individual: latency to explore (measured as the time in minutes between the removal of the separation and when the lizard first stepped into the new environment), per cent time spent in the new environment, and per cent time spent on perches, a behaviour that would make the lizard easier to detect by predators in nature.

MEASURING THE PROPENSITY FOR TAIL AUTOTOMY

We measured the SVL (to the nearest 1 mm) using Mitutoyo digital calipers and the propensity for tail autotomy of each individual (using the method by Fox, Perea-Fox & Franco 1994 and Fox, Conder & Smith 1998) at least 24 h after the second personality trial. To measure the propensity for tail autotomy, we taped a lizard firmly with its abdomen against a rectangular plexiglass plate (20 × 5 × 0·3 cm). We used low residue tapes (3M Scotch tape; 3M, Saint Paul, MN, USA) so that taping would not cause any injury to the lizards. The position of the tail was right over an oval hole (6 × 6 mm) cut through the plate. A thin metal hook (0·8 cm in diameter) attached to a Kistler force transducer (type 9023; Kistler, Winterthur, Switzerland) passed through the hole and pressed on the position at 20% tail length posterior to the cloaca. The hook did not pierce through the tail but simply simulated predatory attempts by applying pressure on the tail surface. One researcher then slowly pulled on the metal hook through the force transducer to gradually exert a force to induce tail autotomy, which always occurred at the point immediately proximal to the force stimulus. The maximum force recorded by the transducer during the process thus represented the propensity for tail autotomy for that individual; the higher the force value, the lower the propensity for tail autotomy. We also measured the diameter of the tail at the point of autotomy from the discarded tail.

STATISTICAL ANALYSES

We only used data from males in all subsequent analyses and performed all statistics in R (version 3·0·3; R Core Team 2014).

To confirm the effectiveness of our dietary treatments, we used a general linear mixed model (function *lme* of the *nlme* package, fitted using the restricted maximum likelihood; Zuur *et al.* 2009) to examine the effect of diet on growth. In the model, we assigned SVL as the response variable and diet and month as fixed factors. We also included individual as a random factor in the model to account for repeated measures.

We performed a principle component analysis (PCA) on the three exploratory behavioural variables (latency to explore, per cent time spent in the new environment and precent time spent on perch) using the *prcomp* function to reduce the number of variables. To examine whether individuals showed consistent boldness in both trials, we used a general linear mixed model, again using the *lme* function, with personality principle component(s) as response variable, trial (first vs. second), diet and SVL as fixed factors and individual as a random factor to reflect repeated measures. We included diet and SVL in the model to examine the possibility that boldness might be influenced by food availability (Dingemanse & Reale 2005) and body size.

To examine the pattern of trait compensation and its relationship with food availability, we used a general linear model with the propensity for tail autotomy (normally distributed and continuous) as the response variable, diet treatment and boldness scores from the first trial (see Results) as predictors and tail diameter as a covariate using the function *gls* (package *nlme*). We identified potential outliers using the criterion of Cook's distance larger than 1 (Bollen & Jackman 1990). We also examined whether our data violated the homogeneity of variance, one of the most important assumptions of linear models, following the procedures in Zuur *et al.* (2009). Partial regression coefficients for each factor from the model would inform us of the significance of a factor independent of the other factors. To examine trait compensation between boldness and the propensity for tail autotomy in more detail, we performed Davies' test to examine a change in the regression slope between size-corrected propensity (residuals from regressing the force to induce tail autotomy against tail diameter) and boldness (Davies 1987). By doing so, we can see if the propensity for tail autotomy increased abruptly when the boldness of an individual passed a certain threshold. Alternatively, both boldness and the propensity for tail autotomy might vary continuously among individuals.

Results

THE EFFECTIVENESS OF DIETARY TREATMENTS

Of all the 59 individuals assigned to each dietary treatment in October 2013, 19 turned out to be male in the restricted diet group and 15 in the unrestricted diet group. From the linear model with those 34 individuals, the effects of month, diet and the interaction term were statistically significant (month: $F_{1,32} = 241{\cdot}61$, $P < 0{\cdot}0001$; diet: $F_{1,32} = 6{\cdot}31$, $P < 0{\cdot}017$; interaction: $F_{1,32} = 23{\cdot}50$, $P < 0{\cdot}0001$). In other words, individuals from both treatments increased in

SVL from October 2013 to January 2014, but those from unrestricted diet group grew significantly more than their restricted-diet counterparts (Table 1). Our dietary treatments therefore were effective in creating a meaningful difference in food availability.

THE EXISTENCE OF BOLD-SHY PERSONALITY

During personality trials, three individuals from each dietary treatment either escaped from the terrarium or pushed through the separation before the end of the 20-min acclimation period. We therefore excluded those individuals from all further analyses, reducing the sample size for the restricted- and unrestricted-diet groups to 16 and 12, respectively. The first principle component (PC 1) on the three exploratory behavioural variables loaded negatively for latency to explore and positively for per cent time in the new environment and accounted for 71% of the total variation; the second component (PC 2) loaded positively for per cent time on perch and accounted for another 28% of the total variation (Table 2). Individuals with higher PC 1 scores were sooner to explore and spent more time in the new environment, and those with high PC 2 scores spent more time staying on perches as opposed to on the substrate. The linear mixed model with either PC 1 or PC 2 as response variable revealed no significant effect of trial, diet, SVL or any of the interactions terms (Table 3, Fig. 1), indicating that *A. sagrei* individuals exhibited consistent boldness between trials and that the degree of boldness was not correlated with food availability or body size.

Table 1. Descriptive statistics of snout-to-vent length (SVL) and tail diameter (at the point of autotomy) of male *Anolis sagrei* under two dietary treatments

	Dietary treatment	
Variables	Restricted	Unrestricted
SVL (mm) October 2013	31·32 ± 1·19	32·47 ± 1·31
SVL (mm) January 2014	38·84 ± 1·60	46·53 ± 0·92
Tail diameter (mm) January 2014	1·70 ± 0·44	2·48 ± 0·78

Values are mean ± SEM. Sample sizes are 19 for restricted diet group and 15 for unrestricted diet group.

Table 2. Results of the principle component analysis (PCA) on three exploratory behavioural variables based on data from 28 individuals

	Loadings	
Behavioural variables	PC 1	PC 2
Latency to explore	−0·656	0·266
% time in new environment	0·656	−0·261
% time on perch	0·373	0·928
Eigenvalue	2·12	0·82
Cumulative variation (%)	70·70	98·00

Table 3. Results of two general linear mixed models with personality PC 1 and PC 2 as response variable, respectively

	Response variables	
Predictor variables	Personality PC 1	Personality PC 2
Trial	1·58 (0·22)	1·35 (0·26)
Diet	0·36 (0·55)	0·87 (0·36)
SVL	1·15 (0·29)	0·70 (0·41)
Trial × diet	0·35 (0·56)	0·01 (0·94)
Trial × SVL	2·88 (0·10)	0·03 (0·87)
Diet × SVL	1·21 (0·28)	0·26 (0·61)
Trial × diet × SVL	0·15 (0·70)	0·01 (0·93)

SVL, snout-to-vent length.
All statistics were $F_{1,24}$ values. *P*-values were given in parentheses. None of the effects were statistically significant.

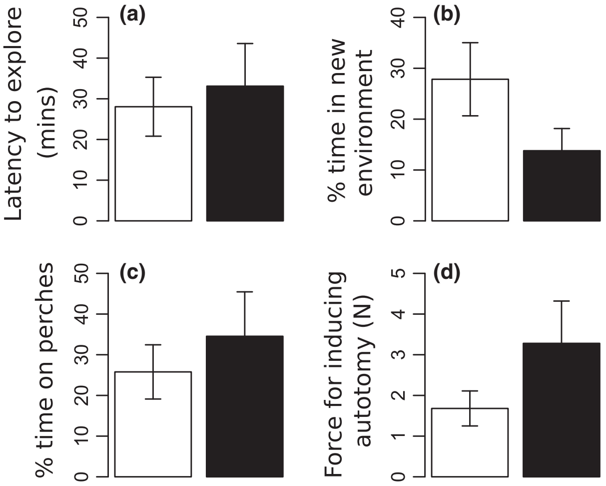

Fig. 1. Bar plots comparing risk-taking behaviour and the propensity for tail autotomy between restricted diet (white bars) and unrestricted diet groups (black bars). Error bars denoted SEM (a) latency to explore (b) per cent time spent in new environment (c) per cent time spent on perches (d) Force needed to induce tail autotomy.

TRAIT COMPENSATION BETWEEN BOLDNESS AND THE PROPENSITY FOR TAIL AUTOTOMY

To minimize the number of variables in the linear model, we used personality PC 1 from the first trial to represent the boldness of individuals. Our rationale was twofold: first, PC 2 had an eigenvalue lower than 1, indicating that it was not a significant component (Peres-Neto, Jackson & Somers 2005). Second, we noticed that, although personality PC scores from the two trials did not differ statistically, individuals tended to be shier in the second trials (Fig. S1, Supporting information), suggesting that the stress induced by the first personality trials might still have had residual effects. We square root-transformed personality PC 1

Table 4. Results of the general linear model examining the effects of personality, diet and tail diameter on the propensity for tail autotomy

Predictor variables	$F_{1,17}$	P-value
Tail diameter	84·14	**< 0·0001**
Personality	9·90	**0·01**
Diet	1·14	0·32
Tail diameter × personality	1·19	0·39
Tail diameter × diet	0·57	0·41
Personality × diet	1·34	0·08
Tail diameter × personality × diet	0·09	**0·03**

Significant effects are in bold. The sample size for this analysis was 28.

scores so that its distribution conformed better to normality before performing statistical analyses. Cook's distance did not reveal any potential outliers, and we did not detect heterogeneity of variance in our data.

The propensity for tail autotomy measured in our study was comparable in magnitude with previous studies on other species of similar body size (Fox, Perea-Fox & Franco 1994; Fox, Conder & Smith 1998). Results of the linear model revealed significant effects of tail diameter and boldness, as well as the interactions terms between all three factors (Table 4). It was harder to induce tail autotomy in lizards with thicker tails. In addition, bolder individuals, regardless of tail size, had higher propensity for tail autotomy, thus supporting our hypothesis of age-independent trait compensation. The effect of diet, however, was not significant (Table 4, Fig. 1). This indicated that food availability did not have any detectable effect on the mean values of boldness and the propensity for tail autotomy. However, a significant three-way interaction in the model led us to examine our data more closely by performing linear regressions between size-corrected propensity for autotomy and boldness separately for each dietary group. Interestingly, the relationship between those two traits differed significantly between the two groups: only individuals raised under unrestricted food exhibited a negative relationship (i.e. trait compensation) (unrestricted group: t = 1·03, d.f. = 14, P = 0·32; restricted group: t = 2·4, d.f. = 10, P = 0·04; Fig. 2). Davies' test, on the other hand, did not reveal any significant change in regression slope, as might be expected if the propensity for tail autotomy changes when boldness exceeds a certain threshold (best at 1·75, k = 10, P = 0·90; Fig. 2).

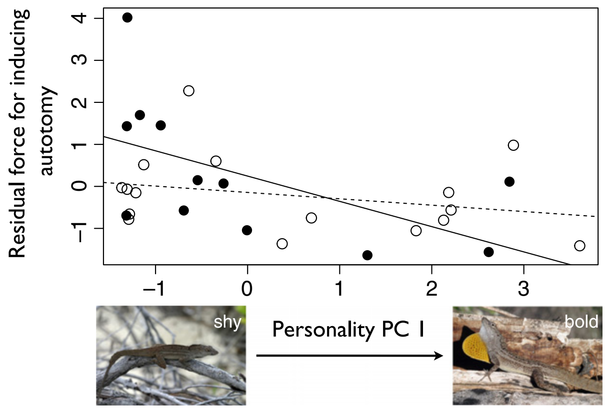

Fig. 2. Distribution of *Anolis sagrei* individuals along exploratory personality PC 1 (boldness) and size-corrected propensity for tail autotomy. Larger values on the x-axis denote bolder personality; higher values on the y-axis denotes higher force required to induce tail autotomy and therefore lower propensity. Open circles and dotted line were individuals from restricted diet group; filled circles and straight line were those from unrestricted diet group. Trait compensation was only obvious in individuals from unrestricted diet group. Individuals in both groups did not form distinct clusters, indicating continuous variation in both traits.

Discussion

There are several key findings from our study. First, we found that bolder *A. sagrei* individuals autotomized their tails more readily and that there was continuous variation in both boldness and the propensity for tail autotomy. Although individuals under different food availabilities on average had similar propensity for tail autotomy and boldness, compensation between the two traits was obvious only among individuals raised with abundant food. Our study is the first to document unambiguous trait compensation among conspecific, similarly aged individuals as well as the first to report how food availability affects the dynamics between two compensatory defence traits. We believe that our results have important implications on several fronts, which we outline below.

IMPLICATIONS FOR THE EVOLUTION OF TRAIT COMPENSATION

Despite the existence of compensatory effects, individuals may still vary in fitness, depending on where they fall on the spectrum of trait compensation (Husak & Swallow 2011). In nature, *A. sagrei* individuals that are too bold might still suffer from lower survival despite the existence of tail autotomy as a compensatory trait, especially if predation intensity is high. Natural selection can thus act on this difference in fitness associated with trait compensation when populations diverge under different predation environments. During the process of population divergence, the defence traits in question might no longer exhibit any variation within each population, although the negative correlation between traits may still exist when comparing populations (Stearns 1992). Results from our study therefore offer valuable information on trait compensation observed at the population and species level by showing for the first time that the same phenomenon occurs among similarly aged conspecific individuals.

Selection on particular combinations of traits might promote the association between the traits in question through proximate mechanisms (Brodie 1992). A number of such proximate mechanisms might help explain the correlation between boldness and the propensity for tail autotomy in our study. First, bolder individuals, due to their risk-prone behaviour, had exposed themselves to predators more often and therefore developed a higher propensity for tail autotomy before being brought back to the laboratory. Alternatively, boldness and the propensity for tail autotomy might be genetically linked or regulated by the same hormone(s) (Brodie 1993); experience, despite its potential to modify the propensity for tail autotomy, is not necessary for establishing the association between these two traits. Given that all the individuals were juveniles with original tails at the time of capture (*c*. 2 months old), we suspect that the role of prior perception of predation risk is likely minor. In addition, it is hard to imagine that the perception of predator risk by any individual would persist throughout the study period when no predator was present, unless an imprinting-like process was involved. Overall, although we cannot completely rule out prior experience as a factor that shapes the observed variation in the propensity for tail autotomy, we suspect that genetics or physiology may play a more prominent role.

IMPLICATIONS FOR THE EVOLUTION OF ANIMAL PERSONALITIES

Sih *et al.* (2004b) proposed that the observed personalities in a population represent constrained evolutionary optima due to behavioural correlations across contexts (see fig. 3b in Sih *et al.* 2004b). The existence of compensatory defence traits can theoretically relax the constraints and allow for a wider range of personality to exist in a population. For example, individuals that would have been too bold to survive may be able to reduce the costs associated with their risk-prone personalities by employing other defence traits. We are not aware of any study that explicitly tested this hypothesis. The closest example to our knowledge is a study comparing defence morphology and boldness in two threespine stickleback populations, where the population with more prominent morphological defence also had greater variation in boldness (Lacasse & Aubin-Horth 2012). Our observation of a positive correlation between boldness and the propensity for employing a defence trait within a population highlights the above-mentioned hypothesis, as any divergence between populations has to originate at the individual level. Studies that examine the variation in risk-prone personality and the degree of defence trait employment across multiple populations or species will offer a more definite answer as to whether compensatory defence traits facilitate the existence of greater variation in animal personality.

THE EFFECT OF FOOD AVAILABILITY ON TRAIT COMPENSATION

An intriguing finding from our study is the existence of trait compensation only when food was abundant. This would suggest that compensating for the bold personality with higher propensity for tail autotomy is only viable when lizards can obtain enough food to quickly regrow the tails. Moreover, it appeared that this result was mainly a consequence of shyer lizards from the unrestricted diet group having lower propensities for tail autotomy (Fig. 2). This finding indicates that food availability indeed affected trait compensation, but not through changing the mean values of the two traits *per se*. Instead, food availability influenced trait compensation in a more subtle manner by altering the degree of variation in the propensity for tail autotomy.

Nevertheless, the fact that lizards from both dietary groups on average did not differ in either boldness or the propensity for tail autotomy warrants further discussions. Adaptive personality theories predict that individuals that are more energetically challenged should be more willing to take risks (Rands *et al.* 2003; Dingemanse & Wolf 2010). One possible explanation for a lack of difference in mean boldness between the two groups of lizards is that although the difference in food level significantly affected growth (see Results), individuals under the restricted diet might not have been energetically challenged enough to significantly change their overall risk-taking tendencies. Alternatively, boldness in *A. sagrei* might be genetically hard-wired and is not plastic within an individual. Although we would like to argue that the former hypothesis is unlikely, a common garden experiment that raises *A. sagrei* individuals in a gradient of food availability is needed for a more definite answer.

Similarly, existing models on the dynamics of inducible morphological defence might help explain why food availability did not affect overall propensity for tail autotomy. A model developed by Higginson & Ruxton (2009) predicted that the use of morphological defence will actually be similar between low and high food availability but peaks when food availability is at intermediate level, provided that the energetic investment in those traits can change over time. However, we also note that tail autotomy differs from classical inducible morphological defence in two major respects. First, the relationship between tail autotomy and the amount of energetic investment is very different from inducible defence traits depicted in existing models, because there is no prior investment needed to enable an individual to autotomize. Second, and perhaps more importantly, a lizard can only employ tail autotomy for a limited number of times throughout its life, whereas such limit does not exist in current models (Steiner & Pfeiffer 2007; Higginson & Ruxton 2009). New models that take those differences into account will provide a more mechanistic interpretation of our result.

IMPLICATIONS FOR FUTURE STUDIES ON AUTOTOMY

Although numerous studies have investigated the variation in autotomy from a cost-benefit perspective (e.g. Cooper & Smith 2009), the importance of food availability in influencing the cost-benefit dynamics of autotomy has not received much appreciation. In addition, although the link between boldness and predation risk has been well-established (Dingemanse & Reale 2005), the effect of boldness on the propensity for autotomy has never been investigated or addressed until this study. We therefore urge researchers seeking to explain the variation in autotomy to include food availability and personality as part of the equation, either through theoretical modelling or experimentally manipulating factors of interest in a laboratory setting in more species capable of autotomy (>80 families of invertebrates, 13 families of lizards, three families of salamanders, at least three snakes species and tuatara *Sphenodon* spp; Wake & Dresner 1967; Arnold 1984; Cooper & Alfieri 1993; Bowen 2004; Fleming, Muller & Bateman 2007; Bateman & Fleming 2009).

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Data accessibility

All data presented in this manuscript are present in the manuscript and its supporting information P8740 (Kuo, Irschick & Lailvaux 2014).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Distribution of *Anolis sagrei* individuals along two measurements of boldness during the first (a and c) and second personality trials (b and d). Values on the *y*-axes are the number of individuals. The upper panel (a and b) shows the result for latency to explore, and the lower panel (c and d) for per cent time spent in the unfamiliar zone. The distribution of individuals shifted towards the right when comparing (a) and (b), indicating the latency to explore was longer during the second personality trials. Similarly, the distribution of (d) is more skewed to the right compared to (c), which indicates that lizards tended to spend less time in the unfamiliar zone during the second personality trials.