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An integrative, cost-benefit analysis on animal perturbations: autotomy and life-history related weight gain

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AN INTEGRATIVE, COST-BENEFIT ANALYSIS ON ANIMAL PERTURBATIONS: AUTOTOMY AND LIFE-HISTORY RELATED WEIGHT GAIN

A Dissertation Presented

by

CHI-YUN KUO

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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The Graduate Program in Organismic and Evolutionary Biology
AN INTEGRATIVE, COST-BENEFIT ANALYSIS ON ANIMAL PERTURBATIONS: AUTOTOMY AND LIFE-HISTORY RELATED WEIGHT GAIN

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DEDICATION

To my parents and OEB
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I would like to acknowledge the Arizona Game and Fish Department, the California Fish and Game Department, the Nevada Department of Wildlife, the Oregon Parks and Recreation Department and the Washington Department of Fish and Wildlife for granting research permits. This dissertation received funding from the University of Massachusetts Amherst, including OEB Research Grant, Natural History Collections Grant, and Doctoral Dissertation Improvement Grant, as well as extramural funding sources, including the Sigma-Xi Grant-in-aid of Research and Human Frontiers Science Program.

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ABSTRACT

AN INTEGRATIVE, COST-BENEFIT ANALYSIS ON ANIMAL PERTURBATIONS:
AUTOTOMY AND LIFE-HISTORY RELATED WEIGHT GAIN

SEPTEMBER 2015

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The variation in behavioral traits and the adaptive significance behind such variation has been a classic question in behavioral ecology. Traits that enhance while simultaneously impose high fitness costs are particularly suitable for addressing this fundamental question, as their expressions are likely under strong selection. In this dissertation, I investigate the variation in a costly antipredator behavior and the underlying cost-benefit mechanisms. The trait of interest is the voluntary shedding of the tail, or tail autotomy, in lizards. Tail autotomy allows lizards to survive close-range encounters with predators but also has severe fitness consequences, including increased energetic demand for regeneration and wound repair, impaired locomotion, lower mating success and reduced long-term survival. The propensity for tail autotomy exhibits remarkable variation both within and among populations, but whether and how this variation reflects the outcome of intricate cost-benefit dynamics has remained poorly understood. The fist chapter uncovers individual variation in locomotor costs following tail autotomy in green anole lizards. Losing the tail affects jump performance in some individuals more than others. In addition, some individuals are able to improve their jump performance over a relatively short period of time whereas others are unable to do so. The second chapter investigates the roles of risk-taking tendency (bold-shy personality) and body condition in explaining the variation in the latter within populations. Using the brown anole lizards, I discover that bolder individuals compensate for their risky behavior by losing their tails more readily. Interestingly, however, such compensatory dynamics only exists when individuals are well-nourished. The third chapter integrates theoretical modeling and field data to examine how ecology (predation, food availability and the intensity of male-male fighting) might drive the variation in tail autotomy across populations. The model predicts that higher predation and food availability both favor higher propensity for tail autotomy, whereas more intense male-male fighting has a stronger yet opposite effect. The model also successfully predicts the pattern of variation in tail autotomy based on the ecological information. The last chapter is a literature review on the interactions between life-history and performance traits in light of the modern ecomorphological paradigm.
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CHAPTER I

INDIVIDUAL VARIATION IN LOCOMOTOR COSTS FOLLOWING TAIL LOSS IN GREEN ANOLE LIZARDS

A. Introduction

Locomotion is involved in almost every aspect of an animal’s daily life and forms a central part of various ecologically relevant activities such as foraging, acquiring mates, and escaping from predators. As a consequence, natural selection often favors high locomotor performance in the wild (reviewed by Irschick et al., 2008). However, animals often encounter situations in nature during which their locomotor performance is severely compromised. For example, in many animal species, females are encumbered with offspring during gravidity and therefore suffer from reduced movement speed and endurance (e.g. Lee et al., 1996; Shaffer & Formanowicz, 1996; Wapstra & O’Reilly, 2001). Locomotor performance may also be greatly reduced when the appendages involved in locomotion are injured or even lost altogether (Fleming, Muller & Bateman, 2007; Bateman & Fleming, 2009; Gillis, Bonvini & Irschick, 2009), although it may require the loss or injury of multiple appendages to cause a significant reduction in locomotor abilities (e.g. Guffey, 1999; Brueseke et al., 2001). The situation of appendage loss is particularly common in animals that can voluntarily discard certain body parts as a strategy to distract or break free from predators (autotomy, McVean, 1975). Autotomy is widespread in the animal kingdom and occurs in a diverse array of invertebrates and some vertebrates (Fleming et al., 2007; Bateman & Fleming, 2009). Moreover, the frequency of autotomy within natural populations can be extremely high [more than 80% of the individuals in some amphipod and lizard populations (Needham, 1953; Van Sluys & Vrcibradic, 2002)]. The widespread occurrence and high incidence of autotomy in natural populations suggest that the reduction in locomotor performance after autotomy can pose a challenge to those species that exhibit this behavior. Although the lost appendage(s) will regenerate in most animals, the rate of the regeneration process varies extensively among taxa, ranging from a few weeks (most
invertebrates) to months (most vertebrates) to around a year in a starfish species (Vitt, Congdon & Dickson, 1977; Pomory & Lares, 2000; Fleming et al., 2007). Therefore, one might expect natural selection to favor mechanisms that enable individuals to rapidly overcome any deficits in reduced locomotor performance after appendage loss. If animals that autotomize can restore impaired locomotor performance before the lost appendages can regenerate, the impact of autotomy on locomotion will only impose a short-term cost to fitness. Conversely, autotomy might impose costs that cannot be quickly remedied, thus resulting in a more substantial impact on locomotor performance and fitness.

One potential short-term solution for animals to compensate for reduced locomotor performance is by making kinematic adjustments. For example, many animals can adjust their kinematics in response to increased loads (Chai & Dudley, 1995; Hoyt, Wickler & Cogger, 2000; Wickler et al., 2001). Humans with muscle injuries also alter the kinematics of other uninjured muscle groups when performing a locomotor task to compensate for reduced overall muscle strength (e.g. Kvist, Good & Tagesson, 2007; Gutierrez et al., 2012). Although it is not clear whether other vertebrates can alter kinematics under similar circumstances in response to injury or the loss of a body part, many non-human vertebrates possess the ability to use muscles differently depending on the context of the locomotor task. For example, toads, cats, and monkeys are all capable of activating forelimb muscles in anticipation to the timing of landings during jumps (Prochazka et al., 1977; Dyhre-Poulsen & Laursen, 1984; Gillis, Akella & Gunaratne, 2010). Therefore, it is reasonable to hypothesize that animals are capable of perceiving appendage loss and compensate for reduced locomotor performance by changing kinematics accordingly.

Several different factors could influence the ability to make effective kinematic adjustments. The first factor is the amount of experience that an animal has for undertaking a particular task following autotomy. In humans and some other mammals, training has been shown
to have striking effects on the ability to perform effectively (e.g. Barbeau & Rossignol, 1987; Dean & Richards, 2000; Tsauo, Cheng & Yang, 2008, but see Fouad et al., 2000), but for most non-mammalian vertebrates, especially for reptiles, the role of training is far more ambiguous (Gleeson, 1979; Tipton et al., 1979; Liu et al., 2009; Busquets et al., 2011). Because strong similarities exist in the sensorimotor mechanisms of locomotion across vertebrates (Rossignol, Dubuc & Gossard, 2006), we can expect that the acquisition of more locomotor experience might facilitate the restoration of locomotor performance following autotomy. On the other hand, humans and some animals show improved locomotor performance following a severe injury simply because the sensorimotor motor system can adjust to the new physical arrangement over time (e.g. Barbeau & Rossignol, 1987). We tested how both factors (locomotor experience and time) influenced the ability of green anole lizards (Anolis carolinensis Voigt, 1832) to jump following tail autotomy, a common occurrence in lizards that has been shown to alter in-air stability during jumping (Gillis et al., 2009).

Anolis carolinensis represents an excellent system to test whether animals that autotomize can compensate for compromised locomotor performance after losing appendages. As a member of the trunk–crown ecomorph (Williams, 1983), A. carolinensis use jumping as their primary means of locomotion (Losos & Irschick, 1996; Irschick & Losos, 1998). Numerous studies have used A. carolinensis to address questions related to locomotor performance and kinematics (e.g. Bels et al., 1992; Toro et al., 2003; Toro, Herrel & Irschick, 2004; Gillis et al., 2009; Kuo, Gillis & Irschick, 2011). As with many other lizards, A. carolinensis commonly autotomize their tails as a way to distract predators or break free from their grasp. The tail is critical in controlling in-air body movement in lizards (e.g. Gillis et al., 2009; Libby et al., 2012), as tailless individuals often exhibited unstable jump kinematics and even awkward landings (Fig. 1.1). Consequently, lower in-air stability and a higher risk of unsuccessful landings after tail loss might create problems for A. carolinensis. For example, an unsuccessful landing may cost a lizard extra time and energy to
return to its habitat, or may cause physical injury or render the lizard vulnerable to predators when it misses the target of landing. Because it can take several months for the tail to fully regenerate (Cox, 1969), lowered in-air stability and its potential fitness consequences suggest that *A. carolinensis* may possess behavioral mechanisms for minimizing the impact of tail autotomy.

In this study, we investigated whether tailless *A. carolinensis* can recover from reduced in-air stability as a function of both time (5 weeks) and the amount of locomotor experience. We hypothesized that both time and locomotor experience after tail loss will facilitate locomotor recovery. Our findings will allow us to better understand whether animals can compensate for impaired locomotor performance after autotomy before the lost appendage can regenerate. More importantly, our results will shed light on whether the costs of autotomy, an important anti-predator strategy, can be ameliorated over relatively short time intervals.

**B. Materials and methods**

We commercially obtained 21 lizards (17 males, four females) with intact and original tails from NC Enterprises (Brooklyn, NY, USA) for our experiment. Lizards were housed individually in terrariums (42.9 × 15.2 × 21.6 cm, length × width × height) with mulch bedding and provided sufficient lighting with 60-W white light bulbs. The size of the terrariums allowed the lizards to move freely but was not large enough for performing full jumps. We sprayed the lizards with water daily and provided them with crickets twice a week (Flukers Farms, Port Allen, LA, USA). We painted white dots (~0.3 cm in diameter, ~1–1.5 cm apart depending on body size) at the positions of pectoral girdle, centre of the trunk, and pelvic girdle on both dorsal and left lateral surfaces of the lizards for digitizing locomotion and extracted performance and kinematic data using computer software (see below).

As male and female *A. carolinensis* do not differ in their jumping abilities once size is taken into account (Lailvaux & Irschick, 2007), we pooled lizards of both sexes and assigned
them randomly into three groups while making the mean snout-to-vent length (SVL) roughly the same across groups. Lizards in the first group (hereafter the tailless-weekly jumping group, mean SVL = 52.9 mm, N = 9) had 80% of their tails removed by grasping the tails with blunt forceps to induce caudal autotomy (Gillis et al., 2009). Lizards in this group were subject to weekly jumping trials for five consecutive weeks. The second group (hereafter the tailless-no weekly jumping group, mean SVL = 53.3 mm, N = 6) had their tails removed in the same manner as in the tailless-weekly jumping group but were only subject to jumping trials in the first and the fifth weeks. The third group (hereafter the control group, mean SVL = 54.31 mm, N = 6) had intact tails and also experienced weekly jumping trials. The control group allowed us to observe any negative effect that our weekly jumping trials might have induced on jump performance (e.g. fatigue and stress). We finished data collection within 5 weeks so that changes in tail length during the study period would not be a confounding factor in this experiment [about 1 cm (10–15% tail length in week 1) by the end of the study period].

In a week, lizards were subject to two rounds of tests, each of which consisted of no more than two consecutive jumping trials. We did not test the animals more frequently because we were concerned about the potential stress to the animals associated with the experimental procedure, especially when data collection had to continue for 5 weeks. The two rounds of tests were at least 60 min apart. Before performing jumping trials, lizards were heated to average body temperatures of 30–32 °C by placing them in a cloth bag in a bucket with a heat lamp located above for 45–60 min. This range of body temperatures has been shown to elicit maximal jumping in *A. carolinensis* (Lailvaux & Irschick, 2007). At the beginning of each jumping trial, we placed the lizards on a platform (11 cm in height) in an arena with raised edges and presented the lizards with a perch 40 cm from the platform as an incentive to jump. The distance of 40 cm was beyond the reach of all lizards and did not interfere with the courses of jumps. Immediately after placing the lizards on the platform, we induced jump behavior by gently tapping their tails. We filmed all
trials at 500 frames s\(^{-1}\) with a Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA) and saved each video into separate AVI files for further analyses.

To analyze jump kinematics, we recorded the body angles at the point of takeoff, 25, 50, and 75% during the aerial phase and at landing, following Gillis et al. (2009). Body angles were measured as the angle between the horizontal and a line connecting the white dots on the side of a lizard. At least two out of three dots were visible at any point of a jump, so we were able to measure all body angles without ambiguity. As *A. carolinensis* exhibited little body bending during the aerial phase of jumps, we believed that this method introduced negligible error to the measurement of body angles. We also calculated the difference between body angles at takeoff and at landing and used it to measure in-air body rotation in a jump. As there was normally three to four jumps for an individual in a given week, we used the mean of each variable from all jumps in the same week to represent the data of individuals for that week. By doing so, each individual had only one value for each variable in any given week.

We first reduced the number of variables by performing a principal component analysis (PCA) on the five body angles (takeoff, 25%, 50%, and 75%, and landing) and used the first principal component (PC1) as a descriptor for overall jump kinematics (see Results). Apart from the first principal component, we also compared landing angle and in-air body rotation among the three groups of *A. carolinensis* individuals, as high values of those two variables signified instability in the air and were two diagnostic features of unsuccessful landings. To see whether the three groups differed in jump kinematics at the beginning of the study period, we used separate one-way analysis of variance (ANOVA) to compare the means of the three variables among the three groups using the data from the first week. We performed the same analysis using the data from the last week to see whether the three groups still differed in jump kinematics at the end of the study period. To determine how jump kinematics changed across the 5-week period, we tested the effect of week on the first principal component, landing angle and in-air body
rotation using separate repeated-measures ANOVAs within each group. In our models, individual was treated as a random factor and week as a fixed factor to account for within-individual variation.

C. Results

PC1 accounted for 79.6% of total variation and loaded strongly for all five body angles (takeoff, 25%, 50%, and 75%, and landing). Therefore, it represented a useful general description of jump kinematics in *A. carolinensis* (Table 1.1). Data for all variables are summarized in Table 1.2. In week 1, the mean of the first principal component did not differ significantly among the three groups (*F*\(_{2,18}=2.25, P=0.13*, Fig. 1.2A). Not surprisingly, there was no significant difference in any of the variables between the two groups of tailless lizards in week 1. However, the control group had significantly lower landing angles and less in-air body rotation (landing angle: *F*\(_{2,18}=8.72, P=0.002*, Fig. 1.2B; in-air body rotation: *F*\(_{2,18}=3.91, P=0.04*, Fig. 1.2C). Lizards with intact tails on average had a landing angle of less than 10° and body rotation of less than 20°, whereas the values of tailless lizards were on average two- to seven-fold higher (Table 2). It is worth noting that the variation in body angles also increased towards later phases of jumps in tailless lizards. Our findings were consistent with those of Gillis *et al.* (2009). Tailless lizards were in general unable to maintain a constant body angle in the air, resulting in more in-air body rotation and higher landing angles.

The difference in jump kinematics and in-air stability among lizards with and without tails still persisted through week 5. Although the mean values of all variables decreased in both the tailless-weekly jumping and tailless-no weekly jumping groups, tailless lizards on average still had more than three-fold higher landing angles and more in-air body rotation than the control group (landing angle: *F*\(_{2,17}=4.23, P=0.03*, Table 1.2, Fig. 1.2E; in-air body rotation: *F*\(_{2,17}=10.03, P=0.001*, Table 1.2, Fig. 1.2F). The first principal component, on the other hand, still did
not differ among the three groups in week 5 \( (F_{2,17} = 0.71, P = 0.51, \text{Fig. 1.2D}). \) One individual died after being tested in week 4, which resulted in the difference in the denominator degrees of freedom of \( F \)-tests between week 1 and 5. One interesting observation from our data was that the difference in body angles between tailed and tailless lizards became more striking towards later phases of a jump (Table 1.2), which was also observed by Gillis et al. (2009). As in the means, the difference in the variation in body angles between the control and the other two groups was still substantial in week 5 (Table 1.2).

The effect of week was not significant for the first principal component, landing angle or in-air body rotation in all linear models, suggesting that the means of the three variables did not differ statistically from week to week in any group (Table 1.3). However, a closer examination of our data revealed extensive individual variation in not only in-air stability itself after tail loss but also the ability to improve in-air stability (Fig. 1.3). The variation among individuals was more notable in the two tailless groups. Some individuals did not seem to suffer from lower in-air stability even in week 1 (e.g., the first individual of the tailless-weekly jumping group), whereas some individuals were more severely affected (e.g. the second to last individual in the tailless-no weekly jumping group). Similarly, some individuals exhibited a gradual decrease in both landing angle and in-air body rotation (e.g. the fourth individual of the tailless-weekly jumping group), whereas some did not show any sign of improvement (e.g. the sixth individual in the tailless-weekly jumping group). The existence of extensive individual variation probably contributed to the lack of statistical difference in the mean values of landing angle and in-air body rotation across weeks.

**D. Discussion**

In general, we found little evidence for improvement in in-air stability during jumping either as a function of the amount of locomotor experience or as a function of time. Indeed, at the
conclusion of 5 weeks, tailless lizards still showed significantly lower in-air stability. At the individual level, however, it appeared that some tailless A. carolinensis individuals did improve their in-air stability substantially (Fig. 1.3). Our findings thus suggest some ability of some individuals to make kinematic adjustments following autotomy, but that overall, A. carolinensis do not seem to recover fully in their jumping ability, even after 5 weeks. This suggests that the loss of a large portion of tail could represent a relatively long-term fitness consequence in A. carolinensis.

The fact that more locomotor experience did not facilitate locomotor recovery in A. carolinensis differs from what has been generally established in humans and other mammals (e.g. Tsauo et al., 2008). This finding is consistent with other studies, which show that training effects for locomotion in lizards are not highly effective, and can even have negative effects (Gleeson, 1979; Garland et al., 1987). However, it is important to consider how our study differs from other studies of injury in mammals and humans. In most studies on mammals, the reduction in locomotor performance was due to neural injuries or illness that damaged sensorimotor pathways. The acquisition of more locomotor experience in those cases helped to enhance muscle strength and/or endurance. In our studies, however, lowered in-air stability was probably the consequence of disrupted jump dynamics after tail loss, with sensorimotor circuits being unaffected (Gillis et al., 2009). Recovering from compromised locomotor performance in tailless A. carolinensis individuals therefore might be more directly related to motor coordination capacity than the amount of acquired locomotor experience. As individuals vary in motor coordination capacity (e.g. Getchell, Forrester & Whitall, 2001; Richards, Mulavara & Bloomberg, 2007), it might explain why individual variation turns out to be the most relevant factor that determines the extent of locomotor recovery in our study.

Animals may experience costs under various circumstances. Costs may arise as a consequence of possessing certain traits (e.g. the conspicuousness costs of aposematic coloration;
Speed & Ruxton, 2010) or may be imposed on the animals by the sociobiological environments (e.g. females in different mating systems; Martin & Hosken, 2003). Costs can also result when animals adopt certain behavioral strategies, such as autotomy (Naya et al., 2007). Regardless of the circumstance, it is reasonable to expect species to have developed compensatory mechanisms to mitigate the most frequently encountered costs. The fact that A. carolinensis seemed unable to recover from reduced in-air stability following tail loss is therefore somewhat surprising, as jumping following tail autotomy should be a fairly common situation in this species. The findings in our study are not only relevant to how A. carolinensis deals with autotomy but may also offer some insight into the distribution of autotomy among vertebrates (see below).

The apparent inability of A. carolinensis to cope with tail loss causes the effect of autotomy to last at least until the tail has re-grown significantly, which may require up to 6 months (Cox, 1969). Poor jump performance, even for a few weeks, thus might have considerable impact on their fitness. For instance, tailless A. carolinensis males might be unable to forage or defend territories as well as individuals with intact tails due to impaired locomotor performance, which could result in reduced mating opportunities. In fact, studies on other lizard species have shown that males suffered from reduced territory size and less mating opportunities after tail loss (e.g. Martin & Salvador, 1993). As anole lizards are short-lived [rarely more than 4 years in nature (Scott, 1984)], forfeiting mating opportunities in even one breeding season could lower their fitness. While our study examined whether A. carolinensis can compensate kinematically for tail loss, there remain other behavioral adjustments that could be important for these lizards. For example, female lizards often change their behavior to become more cryptic during gravidity to compensate for impaired locomotor performance (e.g. Cooper et al., 1990). It is possible that A. carolinensis will behaviorally compensate for the impact of tail loss by moving less often and allowing predators to approach closer before fleeing (reviewed by Bateman & Fleming, 2009). Another possibility would be a modification in habitat use after tail autotomy. For example, it is
possible that *A. carolinensis* would use those parts of the microhabitat that would not require long jumps. All of the above possibilities could be tested with manipulative field studies that follow *A. carolinensis* individuals before and after tail loss. It would also be interesting to examine if the extensive individual variation in locomotor performance following autotomy also occurs in nature, and whether some individuals might be able to recover more quickly than others, thus resulting in lessened impact on fitness.

The results from our study also offer some useful information regarding the occurrence of autotomy among vertebrates. Despite the utility of autotomy during predatory encounters, losing appendages can impose various costs, which may include the loss of energy storage, impaired organismal functions associated with appendage loss, the need of additional energy for regeneration, and altered behavior, to name just a few (see Fleming *et al.*, 2007 for a detailed review). Under those circumstances, a reduction in fitness often results as a consequence of reduced foraging ability and the impaired ability to compete with conspecifics, a lower likelihood to attract mates, higher vulnerability to predators, and even reduced longevity and survival. Thus, the sooner the animals are able to fully regenerate the lost appendages, the sooner those costs will be ameliorated. Therefore, it is not surprising that most species that exhibit autotomy are invertebrates, whose regeneration rate tends to be more rapid (Fleming *et al.*, 2007). Within vertebrates, salamanders and lizards are the two lineages that contain the majority of autotomous species (Fleming *et al.*, 2007). Interestingly, within each lineage autotomy has been lost multiple times (Wake & Dresner, 1967; Arnold, 1984), especially in species which possess other traits that are advantageous during predatory encounters (e.g. larger body size). This trend suggests that autotomy, with its high costs, might be an evolutionary ‘last resort’ for predator defense in salamanders and lizards. Our study lends some support to this view by showing that even for a vertebrate species that commonly autotomizes, the costs of autotomy are not easily remedied.
Comparative studies which test whether species that autotomize more frequently/easily can better compensate for the effect of autotomy would be especially interesting.

Our study demonstrated a general lack of ability to compensate kinematically for reduced in-air stability in tailless *A. carolinensis* individuals but also revealed extensive individual variation in the ability to cope with the locomotor challenge posed by tail autotomy. Thus, it appears that tail autotomy represents a significant and relatively long-term (relative to the lifespan of *A. carolinensis*) cost that is not easily ameliorated. Whether this same pattern holds for locomotor performance for a wide variety of ecologically diverse lizard species is a fruitful avenue for future research. Our findings underline the importance of individual variation in response to a traumatic injury, and in recovery from such an injury.
CHAPTER II

TRAIT COMPENSATION BETWEEN BOLDNESS AND THE PROPENSITY FOR TAIL AUTOTOMY IN BROWN ANOLE LIZARDS

A. 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 behavioral defense 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 behavioral 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 defense.

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 defenseless 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 behavioral and morphological defenses 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 defense 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 defense traits. For example, when food levels are low, investing in morphological defense might become more costly, and individuals might consequently benefit more from risky behavior that enables them to search for new food sources (Steiner & Pfeiffer 2007). The relative investment between morphological defense and risk-taking behavior 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. behavioral defense 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 behavioral and morphological defenses 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 & Fouvopoulos 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 defense 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.

B. Materials and methods

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 was original by its morphology; regenerated tails tended to be shorter, darker in color 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.

We housed *A. sagrei* lizards in individual plastic cages (30 × 16 × 16 cm) with cypress mulch and a perch (30 × 05 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 Results).

In January 2014, we examined boldness in 32 males by observing their exploratory behavior 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 harboring five available perches (30 X 05 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. behavior 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 behavior that would make the lizard easier to detect by predators in nature.

We measured the SVL (to the nearest 1 mm) using a Mitutoyo digital caliper 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.

We only used data from males in all subsequent analyses and performed all statistics in R (version 303; 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 behavioral variables (latency to explore, per cent time spent in the new environment and per cent 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.
C. Results

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: $F_{1,32} = 241.61, P < 0.0001$; diet: $F_{1,32} = 6.31, P < 0.0017$; interaction: $F_{1,32} = 23.50, P < 0.0001$). 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 2.1). Our dietary treatments therefore were effective in creating a meaningful difference in food availability. 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 behavioral variables loaded negatively for latency to explore and positively for percent time in the new environment and accounted for 71% of the total variation; the second component (PC 2) loaded positively for percent time on perch and accounted for another 28% of the total variation (Table 2.2). 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 2.3, Fig. 2.1), 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.

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, suggesting that the stress induced by the first personality trials might still have had residual effects. We square root-transformed personality PC 1 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 2.4). 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 2.4, Fig. 2.1). 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. 2.2). 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. 2.2).
D. 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 defense traits. We believe that our results have important implications on several fronts, which we outline below.

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 defense 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 behavior, 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.

Sih et al. (2004b) proposed that the observed personalities in a population represent constrained evolutionary optima due to behavioral correlations across contexts (see Fig. 2b in Sih et al. 2004b). The existence of compensatory defense 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 defense traits. We are not aware of any study that explicitly tested this hypothesis. The closest example to our knowledge is a study comparing defense morphology and boldness in two threespine stickleback populations, where the population with more prominent morphological defense also had greater variation in boldness (Lacasse & Aubin-Horth 2012). Our observation of a positive correlation between boldness and the propensity for employing a defense 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 defense trait employment
across multiple populations or species will offer a more definite answer as to whether compensatory defense traits facilitate the existence of greater variation in animal personality.

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. 2.2). 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 defense might help explain why food availability did not affect overall propensity for tail autotomy. A model developed by Higgenson & Ruxton (2009) predicted that the use of morphological defense 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 defense in two major respects. First, the relationship between tail autotomy and the amount of energetic investment is very different from inducible defense 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.

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 modeling 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).
CHAPTER III
INTEGRATING MODELING AND FIELD DATA TO EXPLAIN POPULATION-LEVEL VARIATION IN TAIL AUTOTOMY

A. Introduction

A long-standing focus of evolutionary biology concerns how ecology drives adaptive variation through natural selection. Traits that enhance fitness while simultaneously impose high costs are particularly pertinent to this inquiry, as their expressions can be under strong selection (Stearns 1992; Relyea 2002). Autotomy, or the voluntary shedding of body parts (Fredericq 1892), is one of the most extreme behavior within animals. Autotomy allows prey to survive close-range encounters with predators and is employed in more than 100 families of invertebrates and vertebrates, including arthropods, crustaceans, salamanders and lizards (Fleming, Muller & Bateman 2007; Bateman & Fleming 2009). Although autotomy provides clear benefits (predator escape), a substantial body of research also reveals severe short- and long-term costs, including increased energetic demand for regeneration, inferior locomotor performance, lower social status and potentially reduced long-term survival (reviewed in Fleming et al. 2007). Therefore, how readily an individual autotomizes (herein defined as “propensity”) should be regulated by natural selection. Indeed, the extensive variation in the propensity for autotomy, especially among populations, suggests that costs and benefits are balanced in ways determined by the environment (Fleming et al. 2007; Bateman & Fleming 2009). However, without an explicit, cost-benefit analysis, this remarkable variation in autotomy, at least at the population level, still remains an unsolved puzzle.

Much of the existing research on the variation in antipredator traits has focused on plastic, inducible defense traits (Anholt & Werner 1995; Lima & Bednekoff 1999; Teplitsky & Laurila 2007; Steiner & Pfeiffer 2007; Higginson & Ruxton 2009; Cressler, King & Werner 2010). However, findings from these studies are not fully applicable to autotomy, which differs
from the classical inducible defenses in two major respects. First, the cost-benefit dynamics of
autotomy differs fundamentally from that of inducible defenses in that the effectiveness of
autotomy does not depend on energy investment, thereby freeing autotomy from life-history
trade-offs that are at the heart of inducible defenses (Steiner & Pfeiffer 2007; Higginson &
Ruxton 2009). Instead, autotomy is triggered by a force stimulus on the discardable body part.
While the source of the stimulus is often a predator, undesirable autotomy can occur under other
circumstances (see below). This also suggests that natural variation in how readily autotomy
occurs should more directly reflect the different selective regimes in different environments.
Second, autotomy can be under direct regulation of sexual selection, as it can occur during male-
male combat when the discardable body part is used in fighting or is attacked by the rival male
(e.g. Vitt 1981; Maginnis 2006). This further sets autotomy apart from inducible defenses, as well
as most other antipredator traits, in which sexual selection plays a far smaller role.

Previous research has identified three key ecological factors that influence the costs and
benefits of autotomy at the population level: predation intensity, food availability and the
frequency of male-male combat (Arnold 1984; Clause & Capaldi 2006; Maginnis 2006; Bateman
& Fleming 2009). Although each of these factors has been examined in isolation, there has been
no attempt to understand how these three factors together might explain the variation in the
propensity for autotomy among populations. Among the three factors, researchers have devoted
most of their attention towards predation (e.g. Fox, Perea-Fox & Franco 1994; Pafilis et al. 2009).
Other things being equal, the benefit of autotomy should increase with predation intensity.
Therefore, natural selection should favor individuals that autotomize more readily in high
predation environments. On the other hand, although food availability and male-male aggression
have also been explicitly suggested to influence the cost-benefit dynamics of autotomy (Fleming
et al. 2007; Bateman & Fleming 2009), their importance has never been empirically tested. As
food limitation prolongs the regeneration process and thus the duration of the costs following
autotomy, selection should favor lower propensities for autotomy in environments with less food. Lastly, as undesirable autotomy can occur when males fight, environments in which male-male combat is common should favor lower autotomy propensities.

In this study, we integrated modeling and field data to explicitly test how the ecological environment might cause the propensity for autotomy to vary among populations. This integrated approach is a powerful yet rarely used method for providing mechanistic insight into the role of ecology in driving adaptive variation (Gillooly et al. 2001; Núñez-Farfán, Fornoni & Valverde 2007; Dmitriew 2010). We first developed an individual-based model to test the above predictions regarding the roles of predation, food availability and male-male competition on the propensity for autotomy. We then collected data from field populations of side-blotched lizards *Uta stansburiana* and used our model to explain the variation in the propensity for autotomy among those populations. We chose tail autotomy in lizards as our study system because it is one of the most thoroughly studied cases of autotomy (Bateman & Fleming 2009). Moreover, tail autotomy in lizards shares similar cost-benefit features with other systems of autotomy, which ensures that findings from our study will be broadly applicable to explaining the variation in autotomy in other taxa. We used *U. stansburiana* as the study species for its wide geographical distribution, high abundance and the availability of detailed population ecological data (Tinkle 1961; Wilson 1991; Corl et al. 2010).

**B. The model**

We designed the model to approximate the scenarios in which autotomy may occur in nature and in which an individual might experience the benefits and costs of autotomy. We used an optimality approach so that the model could inform us about the propensity that is favored under each specific circumstance.
The model consisted of up to 365 discrete time steps, with each step representing one day in a lizard’s life on which a series of events could occur (Fig. 3.1). First, the lizard had a chance \( P \) to encounter a predator. When predation occurred, the lizard had a probability \( \alpha_p \) to autotomize its tail, which would allow the lizard to survive predation and advance to the next time step with a probability \( S_{tl} \); otherwise, the lizard died of predation. \( S_{tl} \) represented a baseline daily survival rate when a lizard was tailless. When predation didn’t occur, a male lizard might engage in aggressive interactions with another male with a probability \( f \). Under this circumstance, the lizard may autotomize its tail with a probability \( \alpha_b \) and will have a chance \( S_{tl} \) to survive to the next day; a lizard that did not autotomize during male-male combat may live another day with a probability \( S_t \). Since female lizards rarely lose their tails from interacting with other individuals, we set the value of \( f \) to zero when simulating for female lizards. The relationship between \( S_{tl} \) and \( S_t \) is simply \( S_{tl} = c \times S_t \), where \( c \) can assume any value less than one and thus represented the survival cost of tail autotomy. We modeled predation and male-male combat as mutually exclusive events for the sake of simplicity, with the knowledge that a lizard can experience both on any given day in nature.

The values for all model parameters were summarized in Table 3.1. We used the combination of \( S_t = 0.999 \) and \( c = 0.75 \) to simulate high food abundance and \( S_t = 0.998 \) and \( c = 0.6 \) to represent low food abundance. Our rationale was that a food-depleted environment would both cause a reduction in baseline survival and increase the cost of tail autotomy. The value of \( f \) increased incrementally from 0 to 0.01, with higher values denoting higher frequencies of male-male combat. We modeled the relationship between \( \alpha_p \) and \( \alpha_b \) with a generic strictly increasing function:

\[
\alpha_p = \left[ m \cdot \alpha_b / (1 + m \cdot n \cdot \alpha_b) \right] + 0.7,
\]
The first part of the equation (i.e., the part that contains \( m \) and \( n \)) is simply a generic increasing function. We let \( m \) and \( n \) be 10 and 9.5 such that this first component had values from 0.05 to 0.1 as \( \alpha_b \) increasing from 0.01 to 0.2, resulting in \( \alpha_p \) values from 0.75 to 0.8 (Fig. 3.2). This relationship between \( \alpha_p \) and \( \alpha_b \) reflected two facts of tail autotomy (Bateman and Fleming 2009). First, lizards autotomized more readily during predation than during male-male combat, hence \( \alpha_b \) being always greater than \( \alpha_p \). Second, a lizard that autotomized with a higher propensity during predation would also have a higher chance of undesirable autotomy during male-male combat, reflecting the fitness trade-off of having a higher propensity. In addition, we designed the function such that a lizard with extremely low \( \alpha_b \) (e.g. 0.01) would still have a reasonable propensity for autotomy during predation (\( \alpha_p = 0.75 \)) and that \( \alpha_p \) increased quickly and nonlinearly with \( \alpha_b \). We also modeled the relationship between \( \alpha_b \) and \( \alpha_p \) to be linear as an alternative, which yielded qualitatively similar results (See Appendix A). However, the variation of autotomy among field populations was better explained with \( \alpha_b \) and \( \alpha_p \) scaling nonlinearly, and we chose to present those results.

The probability associated with each event did not stay constant at all time steps, as some of the probabilities would change based on prior events. There were mainly two instances where this may happen. First, since the regenerated tail lacks the anatomical feature that enables autotomy, a lizard is only able to autotomize the tail for a limited number of times (Arnold 1983). In the model, we allowed a lizard to lose its tail only three times regardless of the cause; when a lizard that had already autotomized three times encountered a predator or engaged in male-male combats on later days, autotomy would not be a possibility. Second, to reflect the fact that the costs of tail loss diminish as the tail regrows, the survival cost of tail autotomy would only be in effect for 30 days in our model. For example, if a lizard lost its tail on day one, the baseline survival probability would be \( S_{tl} \) instead of \( S_t \) under all circumstances until the end of day 30. It
was possible, however, for the cost of autotomy to persist up to 90 days (e.g., a lizard autotomized on day one, again on day 30, and for the third time on day 60).

We varied the following parameter values to simulate different ecological conditions: predator encounter rate ($P$), baseline survival probability ($S_t$), cost of autotomy ($c$), and the probability of male-male combat ($f$). We ran 1000 simulations with a given combination of parameter values and recorded the percentage of simulations that reached the 365\textsuperscript{th} time step (i.e., the percentage of lizards that survived the whole year). This number represented annual survival ($s$) under each simulated ecological conditions, and we compared those numbers to our own field data as well as values from relevant literature (Wilson 1991; Shine & Charnov 1992) to decide whether our chosen parameter values produced ecologically reasonable outcomes. The values of $s$ ranged from ~30\% in the most favorable ecological condition (i.e., low predation, high food abundance and less male-male combats) to ~3\% when the environment was the harshest, and those values corresponded well with our data and those from the literature (also see Results). Therefore, we were confident that our choice of parameter values adequately represented ecological reality.

With a given set of parameter values (e.g., $P = 0.01$, $S_t = 0.998$, $c = 0.6$, $f = 0$), we let $\alpha_b$ to vary incrementally from 0.01 to 0.2 and ran the simulation for 1000 times for each $\alpha_b$ value. Due to the intrinsic stochasticity in our model, we used locally weighted regressions (LOESS), a multivariate smoothing procedure that facilitated the estimation of a regression surface (Cleveland & Devlin 1988), after plotting survival associated with each $\alpha_b$ value. This allowed us to visualize a fitness curve associated with different propensities for tail autotomy under a particular combination of parameter values, with the optimal propensity defined as the one conferring the highest survival. By systematically varying $P$, $S_t$, $c$ and $f$, we were able to examine
the effects of predation pressure, food availability and the intensity of intrasexual aggression on optimal propensity.

C. Field data

We collected data on predation intensity, food availability, intensity of male-male combat and the propensity for tail autotomy from five populations (Arizona, California, Nevada, Oregon and Washington; Fig. 3.3) of the common side-blotched lizard *Uta stansburiana*. The five populations spanned a wide geographical area and represented different combinations of predation intensity, food availability and the intensity of male-male competition (Table 3.2).

We conducted mark-recapture surveys to obtain our data from March to August of 2012 for populations in Arizona (AZ), Nevada (NV), Oregon (OR) and Washington (WA), and from May to July of 2014 for the population in California (CA). At each site, we caught lizards either by hand or with a noose. We then gave lizards temporary marks by painting a unique number on their backs and clipped their toes as permanent identification. A previous study on the same species showed that paint marking and toe-clipping did not affect survival and could be used with confidence (Wilson 1991). After marking, we measured snout-to-vent length (SVL) and tail length (to the nearest 0.1 mm) and recorded the state of the tail as either original or regenerated based on external morphology (darker color and blunter tips in regenerated tails). At each site, we worked for two weeks or until less than 5% of the individuals were unmarked in a visual census (Dunham, Morin & Wilbur 1988).

We surveyed each population twice, with two surveys ~2 months apart. We calculated daily mortality rate (deaths per 100 individuals per day) at each site as:

\[ 100 \cdot (1 - \frac{k}{N}) \cdot t \] (Dunham et al. 1988),
where \( N \) is the number of individuals marked in the first survey (early activity season); \( k \) the number of marked individuals spotted in the second survey (late activity season); \( t \) the number of days elapsed between two surveys. We then multiplied the daily mortality rate estimated from each site by 60 to obtain the expected mortality over 60 days. This procedure corrected for the difference among sites in the time elapsed between two surveys. Survivorship (\( S \)) over 60 days was then 1 - mortality rate for each site. With the information on survivorship and the percentage of individuals with regenerated tails (\( I \)), we estimated predation intensity (\( i \)) using Schoener’s index (Schoener 1979):

\[
i = \ln(S) / (1 - I).
\]

Schoener’s index uses mortality data and adjusts predation inefficiency by incorporating the frequency of tail injuries in a population. One assumption of Schoener’s index as a proxy for predation intensity is that predation is the only cause of mortality and tail loss. A previous study by Wilson (1991) has shown that predation was the only demographically important cause of mortality over short time scales (e.g., within an activity season) and that emigration was negligible in adult \( U. stansburiana \). Tail loss, on the other hand, can result from predation and intraspecific aggression in males (but not females). This can potentially lead to biased estimation of predation pressure in males due to tail loss from male-male fighting. To avoid such bias, we used tail loss frequency in females when calculating Schoener’s index for both sexes in each population.

Due to difficulty in directly quantifying the intensity of male-male combat, we used the frequency of toe mutilation in males as a proxy (Vervust et al. 2009). During mark-recapture surveys, we recorded whether a male had injured or missing toes. We then calculated the percentage of males with toe mutilations and used it to represent the frequency of male-male combat for that population. We used the total precipitation over the activity season (March to
August) to represent food availability for each population (Dunham et al. 1988; Studds & Marra 2011). We retrieved precipitation data from the National Climatic Data Center (www.ncdc.noaa.gov). When information from the exact location was not available, we used data from the geographically closest weather stations instead (AZ, OR and WA populations).

To not bias our estimation of tail loss frequency and mortality, we captured lizards of both sexes with original tails for collecting propensity data during the second survey. We put captured lizards in individual cloth bags under room temperature (80-85°F) for at least 24 hrs before measuring the propensity for autotomy with the method by (Fox et al. 1994; Fox, Conder & Smith 1998, see also Kuo, Irschick & Lailvaux 2014). We took one lizard at a time from the cloth bag and taped it 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 (1 × 0.4 cm) cut through the plate. A thin metal hook (0.8 cm in diameter) attached to a spring scale 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 applied pressure on the tail surface. We then slowly pulled on the spring scale to gradually exert force on the tail to induce autotomy. We recorded the force read on the scale at the point of autotomy and used the negative value as the propensity to reflect the fact that a higher force stimulus denotes lower propensity. We also measured the diameter of the tail at the point of detachment from the body.

**D. Explaining natural variation in the propensity for tail autotomy**

We first performed a multiple regression with the propensity for tail autotomy as response variable and predation intensity, food availability and the frequency of male-male combat as predictors, done separately for each sex. This helped verify whether the three ecological factors influenced the propensity for tail autotomy in the manner predicted by the model. Since the force
required to induce tail autotomy did not scale with tail diameter within each sex (males: $F_{1,32} = 0.97, p = 0.33$; females: $F_{1,34} = 0.16, p = 0.69$), we used the original force measurement without correcting for tail size. We also did not include interactions terms between predictors due to a limited number of replications (populations).

We then used our model to explain natural variation in the propensity for tail autotomy among populations. For this, we scaled data of predation intensity, food availability, and male-male combat frequency to values appropriate for our model (Table 3.3). We set $P$ to range from 0.005 (for NV females, which experienced the lowest predation) to 0.02 (for WA males, who experienced the highest predation) and linear transformed other groups accordingly. Similarly, we let $f$ be 0.001 for OR males and 0.01 for AZ males, which represented two extremes along the spectrum of male-male fighting, and scaled other populations accordingly using linear mapping. Although annual precipitation varied continuously across the five populations, we assigned the OR population to be the only one that had high food abundance because it was substantially less arid than others. This allowed us to fit the field data to our model while preserving the relative relationships among populations in parameter space. For each population, we ran the simulation for 1000 iterations separately for each sex and recorded the propensity that conferred the highest survival. We repeated the process 20 times for each population/sex combination and calculated the mean. We compared the pattern of variation in mean values between model predictions and field data with a Kolmogorov-Smirnov test for each sex.

**E. Results**

Model simulations showed that high predation intensity and high food availability favored higher propensities for tail autotomy, whereas frequent male-male combat had the opposite effect (Figs 3.4 and 3.5). Interestingly, the frequency of male-male combat most strongly affected optimal propensity for tail autotomy, despite the fact that predation impacted overall
survival to a much higher degree (Fig. 3.4a-c and Fig. 3.5a, d). The effect of predation on the propensity for tail autotomy was the most obvious when intense intrasexual selection had pushed the optimum all the way to the minimum (Fig. 3.4c, f). Overall, the propensity for tail autotomy reflected the cost-benefit optimum of counteracting selection due to intrasexual competition, food availability, and predation intensity.

Field data supported model results; populations with more frequent male-male combats had lower propensities, whereas the effects of the other two factors were nonsignificant (male-male combat: $F_{1,30} = 9.5$, $P = 0.004$, food availability: $F_{1,30} = 0.29$, $P = 0.59$; predation: $F_{1,30} = 0.35$, $P = 0.56$). In females, where predation is the predominant cause of tail loss, populations experienced higher predation pressure had higher propensities for tail autotomy (predation intensity: $F_{1,32} = 6.7$, $P = 0.01$; food availability: $F_{1,32} = 2.96$, $P = 0.09$).

The model predicted that females overall should autotomize more readily than males do (Fig. 3.6a, b). Moreover, the pattern of variation among populations also differed between males and females. The propensity for tail autotomy in males exhibited a north-south gradient, with northern populations having higher propensities. In contrast, the variation among populations in females was far less prominent, although northern populations were still predicted to have slightly higher propensities. Komogorov-Smirnov tests did not reveal any significant difference between model predictions and field data for both sexes (males: $P = 0.08$; female: $P = 0.33$). The lower p-value in males was due to AZ individuals having much higher propensities for tail autotomy than what the model predicted.

**F. Discussion**

By integrating theoretical model and field research, we showed that the optimal propensity for autotomy reflects a balance between predation intensity, food abundance and the degree of male-male competition. High predation and food abundance favor a higher propensity...
for autotomy, whereas more intense male-male competition favors the opposite. Moreover, male-male competition, rather than predation, plays the most critical role in driving the variation in autotomy among populations. Overall, our results suggest that predation likely acts to maintain the ability to autotomize, while male-male competition and food abundance jointly fine-tune the degree of propensity. Aside from the significance to the study of autotomy, we believe that our findings also bear relevance on the ecology of adaptive trait variation.

Although previous research has attempted to study autotomy from a cost-benefit viewpoint, the majority of those studies did not treat autotomy as a trait expressed at the individual level (but see Fox et al. 1994; 1998). Instead, they focused on the percentage of individuals with autotomized body parts in a population and correlated it with other variables of interest (e.g., habitat use, age, sex, etc., see Fleming et al. 2007; Bateman & Fleming 2009 for detailed reviews). Although such approaches helped identify key factors that can affect the occurrence of autotomy, the treatment of autotomy as a population-level trait and the correlational nature of the analyses has nevertheless limited our ability to mechanistically understand the variation in this widely used antipredator trait. Combining simulations and field data, we showed that the optimal propensity for tail autotomy in male U. stansburiana represents a balance between predation pressure, food availability and intrasexual selection. Females, on the other hand, are free from the conflict between losing the tail to predators versus conspecifics, which results in their higher propensities for autotomy.

A particularly interesting finding is that intrasexual selection in the form of male-male combat exerts the strongest influence on the optimal propensity of tail autotomy. Since the formulation of Fisher’s runaway hypothesis (Fisher 1930), the antagonistic roles of natural and sexual selection on phenotypic evolution have been the topic of intensive research. However, the emphasis, when it pertains to predation, has mostly been how predation risk might influence the optimal expression of sexually selected traits (Zahavi 1975; Godin & McDonough 2003; Cothran
To our knowledge, ours is the first study that reports direct influence of sexual selection on the expression of an antipredator trait. The strength of intrasexual selection on the propensity for autotomy might appear counterintuitive at first given that the frequency of male-male combat does not severely affect overall survival. One plausible explanation is that male-male combat occurs more commonly than predation. This, coupled with the fact that autotomy can only be employed for a limited number of times, might result in strong selection against autotomizing in non-predatory scenarios.

Further examination of simulation results revealed two interesting findings. First, the fact that predation significantly increased propensity for autotomy only when the optimal value was at the minimum (Fig. 3.4c, f) implies that predation only acts to maintain the ability to autotomize (i.e. having non-minimal propensity) instead of fine-tuning the propensity for autotomy. Second, the presence of a broad fitness plateau at intermediate levels of male-male combat suggests that populations with intermediate levels of male-male competition might exhibit the highest level of within-population variation in the propensity for autotomy (Fig. 3.4b, e). Those two findings represent new hypotheses for future studies. From our field data, the population with intermediate male-male combat does have the highest variation in the propensity for tail autotomy (Table 3.1), though further data are needed to robustly test this hypothesis.

Although our model was built specifically for the cost-benefit dynamics of tail autotomy in lizards, it can be easily modified for the study of the variation in autotomy in other taxa, especially invertebrates. Autotomy in invertebrates shares similar features with lizards. Most notably, the cost-benefit dynamics of autotomy in invertebrates also hinges upon the interactions between predation, food availability and intraspecific aggression (reviewed in Fleming et al. 2007). However, there are indeed two features of invertebrate autotomy that differ from the lizard system. First, in contrast with tail autotomy, where a lizard incurs the costs immediately after tail loss, the cost of invertebrate autotomy, both short- and long-term, may not be obvious until
multiple appendages are lost (e.g. Guffey 1999; Apontes & Brown 2005). Second, the limitation in the number of times that autotomy can be employed is far more relaxed in invertebrates, where lost appendages regrows after molting and can be autotomized again. Our model can readily accommodate those differences, and it would be an interesting next step to apply our approach to study the variation in the propensity for autotomy in invertebrates. More importantly, we believe that a similar approach can be used for studying the variation in any traits that share similar cost-benefit structure. As an example, a similar model could be designed to examine the variation in optimal group size among allopatric populations or closely related species, which in theory should represent an evolutionary balance between costs and benefits (e.g., cooperative breeding, enhanced defense against predators and higher potential for intraspecific competition; Gaston 1978; Koenig 1981; Whitehouse & Lubin 2005).

While the importance of ecology as the agent of selection has long been recognized, there is a general lack of studies that provide mechanistic links between multiple ecological factors and adaptive trait variation (MacColl 2011). Our study provides one such example and highlights how multiple ecological factors act to drive adaptive trait variation at the population level. Although predation, food availability, and male-male competition vary independently from one another in our model, we note that those factors often covary in nature. For example, habitats with abundant food often sustain more predators (Leibold et al. 1997) and foster higher degrees of male-male competition (Emlen & Oring 1977; Alonso, Magaña & Álvarez-Martínez 2012; Heesen et al. 2014). The five *U. stansburiana* populations exemplify such interplay between ecological factors; habitats that had higher food abundance were generally also under higher predation pressure but less male-male competition (Table 3.1). For instance, the Washington population, due to its favorable food environment, suffered severe predation among the five populations from high abundance of loggerhead shrikes *Lanius ludovicianus* (Kuo, C-Y personal observation; Zani, P personal communication), which might in turn dampen the intensity of male-male competition.
(Table 3.1). The correlation between the three ecological factors might result in their effects counteracting one another, thereby limiting the extent of natural variation in autotomy.

Although our model overall successfully explained natural variation in autotomy in *U. stansburiana*, the mean propensity of AZ males was much higher than the predicted value. Historical events, such as founder effects or population bottlenecks, might be responsible for this observation (Templeton 1980). If males in the AZ population were derived from a small fraction of an ancestral population, it might explain the unexpectedly high propensity for tail autotomy observed in AZ males. Detailed analyses on population genetics will provide insight into this hypothesis. In addition, although both model predictions and field data revealed a general north-south gradient in the propensity for tail autotomy, we note that such latitudinal trend is the result of complex dynamics involving multiple interacting forces. Our study therefore underscores the importance of understanding trait variation with a mechanistic approach through identifying the individual role of each relevant factors, and how these factors interact.
CHAPTER IV

LIFE-HISTORY RELATED WEIGHT GAIN IN THE MODERN
ECOMORPHOLOGICAL PARADIGM

A. Introduction

Over the past four decades, the theories of life history and ecomorphology have emerged independently as two major paradigms seeking to explain how organisms achieve optimal fitness. Life-history theory primarily focuses on how the dynamics of resource allocation shape the tempo and mode of reproductive investment (Gadgil & Bossert 1970; Charlesworth & Leon 1976; Stearns 1977), whereas the theory of ecomorphology posits that an organism’s fitness is tightly linked to how well it can perform ecologically relevant tasks, such as acquiring resources, escaping predators and competing for mates (Bartholomew 1958; Arnold 1983; Bennett & Huey 1990; Garland & Losos 1994; Irschick, Meyers & Husak 2008). A recent expansion of the ecomorphological paradigm, however, has united these two frameworks and placed performance traits in the nexus of life-history trade-offs (Lailvaux & Husak 2014). This updated ecomorphological paradigm points out ways through which whole-organism performance traits may interact with key life-history events, most notably resource acquisition and reproductive investment (Fig. 3 in Lailvaux & Husak 2014). Resource acquisition affects performance traits by determining the size of the resource pool available for performance related tissue development (e.g., bones, muscles, etc), whereas reproductive investment represents a competing resource allocation pathway. Other things being equal, the more resource an individual acquires, the better it will be able to perform ecologically relevant tasks. On the other hand, every increment of resources allocated for reproduction theoretically leads to a decline in performance related investment, thereby creating trade-offs between reproductive output and performance capacities.
Although Lailvaux and Husak (2014) has outlined ways in which resource acquisition and reproductive investment may influence performance capacities via allocation trade-offs, these two life-history events can interact with whole-organism performance through a more direct, functional mechanism. In many species, resource acquisition and reproductive investment inevitably cause substantial and prolonged weight gain (e.g. Table 3 in Kuo, Gillis & Irschick 2011), which can greatly increase the energetic cost of locomotion as well as alter the kinematics of movement (Kram 1996; Hoyt, Wickler & Cogger 2000; Wickler et al. 2001; Irschick et al. 2003; Kuo et al. 2011). As a result, significant weight gain under those circumstances can cause severe reductions in locomotor capacities. Moreover, the degree of locomotor impact should theoretically be proportional to the amount of weight gain, which normally reflects an individual’s foraging effort (the amount of food consumption) or reproductive investment (offspring number/size). This clearly creates trade-offs between these two key life-history events and whole-organism performance through mechanisms unrelated to resource allocation. Although such functional trade-offs have never been discussed in the context of ecomorphology, we argue that their inclusion in the modern ecomorphological paradigm is necessary as they present alternative pathways along which life-history and performance traits interact and evolve.

Aside from supplementing the existing ecomorphological paradigm, weight gain from foraging and reproduction allows us to test comparative hypotheses concerning the dynamics between life-history and performance traits. Two factors of prime importance are body size (mass) and macrohabitat (terrestrial, aquatic and aerial). Body size is widely used in biological scaling to explain the variation in metabolism, kinematics and energetics, all of which play crucial roles in animal locomotion (Dickinson et al. 2000; Alexander 2003). In general, larger animals have higher metabolic demands (Speakman 2005), suggesting that they might need to consume more food and thus might experience more foraging related weight gain. On the other hand, although comparative dataset for relative clutch mass (i.e. reproductive investment) exists
for several major clades (e.g. Rahn, Paganelli & Ar 1975; Vitt & Price 1982; Duarte & Alcaraz 1989), there is no single law that determines how clutch mass should scale with body size across major taxonomic groups. Macrohabitat is one of the defining features of an organism’s ecological environment and to a large extent dictates the mode of locomotion. A general pattern is that aquatic locomotion imposes the least cost of transport (defined as the energy required to move one unit body mass one unit distance), followed by aerial locomotion and then by terrestrial locomotion (Alexander 2003). This also implies that aquatic species might experience the least constraint in the amount of weight gain and that their locomotion might be impacted the least by increase in body mass, with aerial and terrestrial species following in order. Comparing life-history related weight gain and locomotor impairment among species that differ in macrohabitat therefore would offer insight into the role of ecology in shaping the interactions between life-history traits and performance capacities.

Foraging and reproduction related weight gain also offers opportunities to broadly examine how behavior and physiology can modify the morphology-performance-fitness gradient. Evolutionary biologists have long recognized the importance of behavior in mediating evolution (Plotkin 1988; Huey, Hertz & Sinervo 2003; Duckworth 2008). Garland and Losos (1994) also argues that behavior acts as an intermediacy between performance and fitness and is the most direct target for selection. On the other hand, physiology has been traditionally recognized to regulate performance through trade-offs mediated by hormonal pathways. The most notable example is the widely established role of testosterone in enhancing performance at the expense of immune functions (e.g., Miles et al. 2007). However, there exist other physiological mechanisms that modify the morphology-performance-fitness gradient (see D.1 Physiological mechanisms). As we will show in this review, animals have evolved several behavioral and physiological mechanisms that alleviates weight gain related fitness impact. Weight gain associated with
foraging and reproduction therefore highlights how behavior and physiology modify the relationship between morphology and performance, and that between performance and fitness.

In this review, we first provide a summary of quantitative data on the amount of weight gain due to feeding and reproduction, as well as the degree of locomotor impairment that ensues. We also summarize behavioral and physiological mechanisms that help alleviate the fitness consequences of compromised locomotion. This summary of literature aims to demonstrate the range of taxa that experience functional trade-offs between life-history and performance traits, as well as offering a broad, comparative picture on the extent of weight gain and the degree of locomotor impairment following feeding and reproduction across a multitude of taxa. We also address two comparative questions regarding the relationship between weight gain and locomotor impairment: (1) how would the relationship between weight gain and locomotor impairment change over a wide range of body size? and (2) among animals that move on land, in water and in the air, which group experiences the most substantial weight gain and which one suffers the most severe locomotor impairment? We conclude this review with a synthesis based on our meta-analyses and outline potential directions for future research.

**B. Materials and methods**

We focused on locomotor performance traits (speed, endurance, etc) for the integral role of locomotion in animal ecology and its amenability to be influenced by weight gain (Alexander 2003). To compile the dataset, we searched ISI Web of Science database using the following keyword combinations: food and locomotion, feeding and locomotion, reproduction and locomotion, cost of reproduction, egg and locomotion, as well as references from papers found using keyword searches. From the available studies, we excluded those that did not provide quantitative information on either weight gain or locomotor impairment for the purpose of meta-analyses.
We extracted data on body mass, the amount of weight gain (as percent body mass), and the degree of performance impairment from qualified papers. We performed comparative meta-analyses on squamate reptiles and birds because these two were the only groups with sufficient data. Interestingly, studies on squamates mostly focused on weight gain associated with pregnancy and its performance consequences, whereas those on birds tended to focus on weight gain related to resource acquisition. As species did not represent independent data points, we used phylogenetic generalized least squares (PGLS, Grafen 1989) when examining the body mass-weight gain and weight gain-performance impairment relationships within these two groups. We obtained the phylogeny of squamate reptiles from Pyron, Burbrink & Wiens (2013). Since only a backbone phylogeny was available for all avian species, the analyses on birds were performed on 100 pseudo-posterior samples from the phylogeny by Ericson (2012)(see Jetz et al. 2012 for methodological details). The generation of pseudo-posterior phylogenies was performed through the web server Bird Tree (birdtree.org). We reported the median F- and P-value from the 100 PGLS results when assessing whether there was a significant relationship between body mass and relative weight gain, and between relative weight gain and the degree of performance impairment.

C. Life-history related weight gain and performance consequences

C.1 Reproduction

Reproduction most commonly induces weight gain in the form of developing offspring, and the amount of weight gain is often quantified as relative clutch mass (RCM). Variation in RCM has been documented in numerous major taxonomic groups (insects: Wickman & Karlsson 1989; fish: Duarte & Alcaraz 1989; squamate reptiles: Vitt & Price 1982; Shine 1992; 2005; birds: Rahn et al. 1975; Martin et al. 2006). The reduction in locomotor performance from developing offspring has been explicitly recognized as a major cost of reproduction in some taxa, although functional trade-offs between reproductive investment and locomotor performance has
been documented in scorpions, fishes, salamanders, squamate reptiles, birds and mammals (Table 1). Available quantitative data revealed a ten-fold difference in the amount of relative weight gain among taxa, ranging from 7% in starling *Sturnus vulgaris* (Lee, Witter & Cuthill 1996) to 70% in the common lizard *Zootoca vivipara* (Bauwens & Thoen 1981; Van Damme, Bauwens & Verheyen 1989). The degree of performance impairment also varies markedly from 10% (flight speed in zebra finches *Taeniopygia guttata*) to 60% (endurance in garter snakes *Thamnophis marcianus*).

In some primates, the functional trade-off between reproductive investment and locomotor performance can persist well after parturition, as females carry their young for an extended period of time. Studies on chimpanzee (*Pan troglodytes*), spider monkey (*Ateles belzebuth belzebuth*) and tamarin (*Saguinus oedipus*) have revealed that neonate carrying can reduce the mother’s travel speed, though quantitative data on the amount of weight gain and performance impairment were scarce (Wrangham 2000; Shimooka 2005; Caperos *et al.* 2012). Neonate carrying also impairs running speed in female common striped scorpions (*Centruroides vittatus*) (Shaffer & Formanowicz 1996). Direct, functional interactions between reproduction and locomotor performance were not limited to females. In seahorses and pipefishes, male was the sex that carried developing offspring (Wilson *et al.* 2001). In those species, functional trade-offs between reproductive investment and locomotor performance should be more profound in males.

**C.2 Resource acquisition**

Acquiring resources, most often through foraging, is crucial for tissue development that are necessary for locomotion, as well as providing energetic fuel for performing locomotor tasks. Indeed, body mass increase through foraging has traditionally been considered to reflect a better individual’s nutritional state (Jakob, Marshall & Uetz 1996; Schulte-Hostedde *et al.* 2005; Stevenson & Woods 2006; Peig & Green 2010), However, foraging can lead to temporary yet
severe reductions in locomotor performance in species where a regular meal can induce substantial weight gain. The most extreme cases occurred in two invertebrates: the mosquito *Anopheles gambiae* and the medicinal leech *Hirudo verbana*, which could increase body mass by 200% and 500%, respectively, after regular feeding events (Roitberg 2003; Claflin *et al.* 2009). In *H. verbana*, such weight gain reduced swimming speed by 72%. Two studies also documented similar phenomenon in snakes (Garland & Arnold 1983; Martin 1996), although the degree of performance impairment was less extreme. Functional trade-off between resource acquisition and locomotor performance was best documented in birds, as numerous bird species experienced regular fluctuations in body mass both over short and long time scales. Unlike most other animals, weight gain associated with foraging in birds was not directly due to the mass of food items but rather arose as a result of metabolite assimilation, mainly in the form of fat. Short-term fluctuations in bird body mass could occur within the course of a day. This phenomenon was especially prominent in small birds, whose body mass could differ by 7% between dawn and dusk (Metcalf & Ure 1995). Over a longer time scale, body mass in birds could vary more substantially as they accumulated metabolic fuel for migration or overwintering (as much as 60%, Kullberg, Fransson & Jakobsson 1996; Kullberg, Jakobsson & Fransson 2000; Krams 2002). Overall, performance impairment from weight gain exhibited extensive variation, ranging from 4.5% in the great tit *Parus major* (flight speed, Krams 2002) to 34% in juvenile garter snakes *Thamnophis elegans* (endurance, Garland & Arnold 1983).

### C.3 Dynamics between weight gain and performance impairment

Although both the amount of weight gain and the degree of locomotor impairment exhibited extensive variation across taxa, the amount of weight gain was not correlated with body mass in both squamates (PGLS, $F_{1,13} = 0.01$, $P = 0.94$) and birds (PGLS with 100 pseudo-posterior phylogenies, median $F_{1,5} = 0.73$, median $P = 0.43$). In addition, gaining more weight overall did not result in more severe reduction in locomotor performance in both groups (squamates, PGLS,
$F_{1,13} = 0.41, P = 0.53$; birds, PGLS with 100 pseudo-posterior phylogenies, median $F_{1,5} = 0.08$, median $P = 0.79$). Interestingly, weight gain seemed to impact endurance more than speed, at least in terrestrial locomotion, although the number of observations was small (circles vs. squares in Fig. 2). In addition, weight gain induced similar degrees of impairment in terrestrial and aquatic locomotion (terrestrial: 30%; aquatic: 31%, excluding $H. verbana$), whereas locomotor performance in birds was less affected (21%), likely due to lower relative weight gain compared to other taxa (symbols of different colors in Fig. 2).

### D. Mechanisms modulating the interactions between life history and performance

Animals have evolved several mechanisms to reduce the fitness impact following life-history related weight gain. Those mechanisms belonged to two broad categories: physiological and behavioral. These two types of mechanisms play distinct roles in modulating the morphology-performance-fitness gradient; physiology may alter the linkage between morphology and performance or that between performance and fitness, whereas behavior generally mediates the relationship between performance and fitness (Fig. 1). We outline those mechanisms in more detail below.

#### D.1 Physiological mechanisms

Birds represent the best documented examples of physiology modulating the morphology-performance-fitness gradient. Some birds have evolved physiological mechanisms that regulate the timing of metabolite assimilation such that weight gain only occurred when the expected fitness impact was low. As an example, a manipulative field study in the great tit *Parus major* revealed that individuals significantly delayed fat assimilation until later hours of the day only when a simulated predator was present (MacLeod, Gosler & Cresswell 2005b). Such physiological mechanism allows individuals to avoid weight gain and resulting locomotor impairment when predators were active. Another study found that blackbirds *Turdus merula* had
different fat assimilation schedules in the summer and in the winter (MacLeod et al. 2005a). In blackbirds, weight gain occurred in the morning during the winter and shifted to occur just after dawn and before dusk in the summer. Such a seasonal difference in the timing of fat assimilation presumably evolved as an optimal strategy to balance the risks of starvation versus predation. In the winter, when predators were less active and the risk of starvation was high, individuals would benefit from storing fat earlier in the day. During the summer, however, the ecological conditions reversed (low starvation and high predation risk), individuals would benefit from delaying weight gain until the peak of predation risk has passed. In those species, physiology allowed life-history related weight gain (and resulting locomotor impairment) to have different fitness consequences by modifying the link between performance and fitness.

Migrating birds used a different physiological mechanism to cope with weight gain associated with fuel load. Several migratory birds increased flight muscle mass in conjunction of storing fat prior to the commencement of long-distance flight (reviewed in Lind, Jakobsson & Kullberg 2010). A simultaneous increase in flight muscle mass and fuel load therefore minimized the decrease in wing loading, thereby allowing the birds to maintain similar flight performance in the face of weight gain. In those cases, physiology modulated the morphology-performance gradient by creating a many-to-one mapping between morphology and performance (lean individuals with low flight muscle mass vs. fat individuals with high flight muscle mass).

**D.2 Behavioral mechanisms**

One major fitness consequences of locomotor impairment is higher vulnerability to predation (Irschick et al. 2008). Behavioral changes under increased predation risk have been the topic of numerous theoretical and empirical research. A few theoretical models explicitly posited that individuals with inferior locomotor performance suffered disproportionately higher predation risk and predicted three major ways in which animals can compensate behaviorally: staying in
safer habitats, forgoing/delaying feeding to reduce exposure to predation, or becoming behaviorally more cryptic (McNamara, Houston & Lima 1994; Bednekoff 1996; Lima & Bednekoff 1999; Lind 2004; Brodin 2007). Indeed, studies on birds and lizards have provided much support to those predictions. Blackcaps (Sylvia atricapilla) that had gained more weight prior to migration were less willing to stay on a risky patch when exposed to predation (Fransson & Weber 1997). Similarly, gravid female collard lizards (Crotaphytus collaris) compensated for locomotor impairment by staying closer to refugia (Husak 2006). Studies on redshanks, great tits, and yellowhammers revealed that individuals perceiving higher predation risk often forewent or delayed feeding such that weight gain associated locomotor impairment would have less severe fitness consequences (van der Veen 1999; Gentle & Gosler 2001; Cresswell & Whitfield 2008). Regarding increased crypsis under weight gain, a study on the gray catbird Dumetella carolinensis showed that fatter birds remained motionless for longer after being exposed to a simulated predator (Cimprich & Moore 2006). Numerous studies on squamates, especially lizards, have also demonstrated that individuals experiencing locomotor impairment due to feeding or gravidity tended to remain motionless and allowed predators to approach closer before escaping (e.g., Cooper et al. 1990; Martin 1996; Brown & Shine 2004).

E. Synthesis and future directions

A recent revival of the ecomorphological paradigm places whole-organism performance in a life-history framework, where whole-organism performance, life-history and physiological traits are connected through resource allocation pathways. Our review summarizes empirical data on life-history related weight gain and subsequent locomotor impairment in the light of the modern theory of ecomorphology, while at the same time supplements this expanded paradigm by showing that two of the major life-history events, resource acquisition and reproductive investment, can interact with performance traits through mechanisms unrelated to resource allocation. Data from the literature reveals that weight gain from foraging and reproduction has
far-reaching consequences on whole-organism performance, affecting multiple types of locomotor performance traits, in different macrohabitats (terrestrial, aquatic and aerial), and across a wide range of taxa (from leaches to mammals). However, in squamates and birds the amount of weight gain is not correlated with body mass, nor can it explain the degree of locomotor impairment. In the face of substantial and prolonged weight gain, animals have evolved several physiological and behavioral compensation mechanisms that modulates both the morphology-performance and performance-fitness gradients. Below we present a synthesis from our literature review and meta-analyses, as well as outline potential directions for empirically studying whole-organism performance in the context of life history evolution.

### E.1 Kinematics and nonlinearity of the morphology-performance-fitness gradient

A number of studies have pointed out that the morphology-performance-fitness mappings may deviate from a one-to-one relationship (e.g. Wainwright et al. 2005). The mediating roles of physiology and behavior in the ecomorphological paradigm further strengthens the view that the morphology-performance-fitness relationship can be highly nonlinear. Examples from birds and squamate reptiles have highlighted the fact that individuals differing in morphology (e.g. with vs. without weight gain) do not necessarily vary in performance and/or fitness. Physiology and behavior can thus relax the selective pressure on performance and may potentially slow the pace of performance evolution. One way to test this hypothesis is to compare the strength of selection on performance traits of interest between the times when individuals are experiencing weight gain and when they are not. If physiological and behavioral compensation mechanisms do significantly reduce the adversary effect of weight gain on fitness, the strength of selection should be similar in both cases.

Another promising direction for future research is to further explore the role of kinematics in modulating the relationship between morphology and performance under weight
gain situations. In fact, applying artificial loads to induce weight gain has been a common approach to induce kinematic changes during locomotion in various animals, including humans (e.g. Kram 1996; Wickler et al. 2001; Irschick et al. 2003; Lee et al. 2004; McGowan et al. 2006; Seven, Akalan & Yucesoy 2008). However, many of those studies apply artificial loads in ways that do not conform to ecological reality, and as a consequence their results, though insightful, do not provide direct answer as to how animals might change kinematics to maintain the same level of performance under natural weight gain. On the other hand, most studies that examined performance consequence of weight gain did not record detailed kinematic information. We therefore urge future studies to bridge this gap by combining the strengths of performance and kinematic studies and to provide mechanistic insights into nonlinearity between morphology and performance.

E.2 The ecology of the ecomorphological paradigm

The role of ecology in the ecomorphological theory, though essential, has always rested at the individual level, with a focus on an animal’s ability to perform ecologically important tasks (Arnold 1983; Bennett & Huey 1990; Lailvaux & Husak 2014). Considering the well-established role of ecology in prompting the diversification of morphological, locomotor and life-history characters, it is surprising that we still have not moved very far since Stearns’s (2000) resounding urge to study the macroevolution of life history. The recent union of ecomorphology and life-history theories offers an ideal system, both conceptual and empirical, that allows us to examine how performance and life-history traits interact in a macroevolutionary light. Indeed, Lailvaux and Husak (2014) points out that the structure of the modern ecomorphological paradigm is likely to vary among species. We echo their statement and further argue that weight gain associated with resource acquisition and reproductive investment, due to its occurrence in a wide variety of taxa, would serve as an excellent platform for investigating how ecology might shape the macroevolution of ecomorphological dynamics.
Our meta-analyses presents a promising direction for more comparative studies. Although our analyses on birds and squamates did not find strong correlations between body mass, relative amount of weight gain, and the degree of performance impairment, it is possible that the range of body mass variation in our dataset is still not enough for detecting any pattern. Moreover, quantitative data on locomotor impairment following weight gain are generally lacking for aquatic species. Although we have attempted to compare the dynamics between life-history related weight gain and locomotor impairment across major groups, the inequality in the amount of data among groups limits our ability to interpret our results. Future studies should prioritize on collecting data from groups other than squamate reptiles and birds, where empirical data are scarce.
Table 1.1: Factor loadings of the first two principal components and the cumulative amount of variation explained

<table>
<thead>
<tr>
<th>Variable</th>
<th>Loadings</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(Body angles)</td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>Takeoff</td>
<td>0.356</td>
<td>0.744</td>
<td></td>
</tr>
<tr>
<td>25% aerial phase</td>
<td>0.473</td>
<td>0.320</td>
<td></td>
</tr>
<tr>
<td>50% aerial phase</td>
<td>0.491</td>
<td>-0.133</td>
<td></td>
</tr>
<tr>
<td>75% aerial phase</td>
<td>0.474</td>
<td>-0.298</td>
<td></td>
</tr>
<tr>
<td>Landing</td>
<td>0.430</td>
<td>-0.488</td>
<td></td>
</tr>
<tr>
<td><strong>Eigenvalue</strong></td>
<td>1.996</td>
<td>0.928</td>
<td></td>
</tr>
<tr>
<td><strong>Cumulative variation (%)</strong></td>
<td>79.6</td>
<td>96.8</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.2: Jump performance and kinematic variables for the three groups at the beginning (week 1) and the end (week 5) of the study period; values are means ± SEM

<table>
<thead>
<tr>
<th></th>
<th>Week 1</th>
<th>Week 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Tailless-weekly jumping</td>
</tr>
<tr>
<td>Body angles (degree)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Takeoff</td>
<td>13.41±1.96</td>
<td>10.70±0.56</td>
</tr>
<tr>
<td>25% aerial phase</td>
<td>17.14±2.09</td>
<td>23.52±1.08</td>
</tr>
<tr>
<td>50% aerial phase</td>
<td>15.89±2.26</td>
<td>36.85±1.79</td>
</tr>
<tr>
<td>75% aerial phase</td>
<td>16.36±2.56</td>
<td>46.02±2.41</td>
</tr>
<tr>
<td>Landing</td>
<td>5.43±1.97</td>
<td>51.72±2.93</td>
</tr>
<tr>
<td>In-air body rotation (degree)(^a)</td>
<td>16.99±0.74</td>
<td>39.87±0.91</td>
</tr>
</tbody>
</table>

\(^a\)The difference in body angles between takeoff and landing.
Table 1.3: Summary of statistics from generalized linear models that tested for the effect of week on the first principal component (PC1), landing angle (θ_L) and in-air body rotation (Δθ) within each group; the effect of week was not significant for all three variables in all groups.

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Tailless-weekly jumping</th>
<th>Tailless-no weekly jumping</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>θ_L</td>
<td>Δθ</td>
</tr>
<tr>
<td>F</td>
<td>3.15</td>
<td>0.07</td>
<td>2.56</td>
</tr>
<tr>
<td>d.f.</td>
<td>1, 27</td>
<td>1, 27</td>
<td>1, 27</td>
</tr>
<tr>
<td>p</td>
<td>0.08</td>
<td>0.79</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Table 2.1: Snout-to-vent length (SVL) and tail diameter (at the point of autotomy) of male *Anolis sagrei* under two dietary treatments

<table>
<thead>
<tr>
<th>Variables</th>
<th>Diet treatment</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Restricted</td>
<td>Unrestricted</td>
<td></td>
</tr>
<tr>
<td>SVL (mm) October 2013</td>
<td>31.32 ± 1.19</td>
<td>32.47 ± 1.31</td>
<td></td>
</tr>
<tr>
<td>SVL (mm) January 2014</td>
<td>38.84 ± 1.60</td>
<td>46.53 ± 0.92</td>
<td></td>
</tr>
<tr>
<td>Tail diameter (mm) January 2014</td>
<td>1.70 ± 0.44</td>
<td>2.48 ± 0.78</td>
<td></td>
</tr>
</tbody>
</table>
### Table 2.2: Results of the principle component analysis (PCA) on three exploratory behavioral variables based on data from 28 individuals

<table>
<thead>
<tr>
<th>Behavioral variables</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latency to explore</td>
<td>-0.656</td>
<td>0.266</td>
</tr>
<tr>
<td>% time in new environment</td>
<td>0.656</td>
<td>-0.261</td>
</tr>
<tr>
<td>% time on perch</td>
<td>0.373</td>
<td>0.928</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>2.12</td>
<td>0.82</td>
</tr>
<tr>
<td>Cumulative variation (%)</td>
<td>70.70</td>
<td>98.00</td>
</tr>
</tbody>
</table>

### Table 2.3: Results of the general linear model examining the effects of personality, diet and tail diameter on the propensity for tail autotomy
Table 2.4: Results of the general linear model examining the effects of personality, diet and tail diameter on the propensity for tail autotomy. Significant effects are in bold. The sample size for this analysis was 28.
<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>$F_{1,17}$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail diameter</td>
<td>84.14</td>
<td>$&lt;0.0001$</td>
</tr>
<tr>
<td>Personality</td>
<td>9.90</td>
<td>0.01</td>
</tr>
<tr>
<td>Diet</td>
<td>1.14</td>
<td>0.32</td>
</tr>
<tr>
<td>Tail diameter $\times$ personality</td>
<td>1.19</td>
<td>0.39</td>
</tr>
<tr>
<td>Tail diameter $\times$ diet</td>
<td>0.57</td>
<td>0.41</td>
</tr>
<tr>
<td>Personality $\times$ diet</td>
<td>1.34</td>
<td>0.08</td>
</tr>
<tr>
<td>Tail diameter $\times$ personality $\times$ diet</td>
<td>0.09</td>
<td><strong>0.03</strong></td>
</tr>
</tbody>
</table>

Table 3.1: Summary of parameter values in the model
Table 3.2: The ecological environment and propensity for tail autotomy in males and females of five *Uta stansburiana* populations

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P$</td>
<td>Predator encounter rate</td>
<td>0.01, 0.015</td>
</tr>
<tr>
<td>$f$</td>
<td>Frequency of male-male combat</td>
<td>0-0.01</td>
</tr>
<tr>
<td>$S_t$</td>
<td>Daily survival when with a tail</td>
<td>0.999, 0.998</td>
</tr>
<tr>
<td>$c$</td>
<td>Costs of autotomy</td>
<td>0.75, 0.6</td>
</tr>
<tr>
<td>$\alpha_b$</td>
<td>Baseline propensity for tail autotomy</td>
<td>0.01-0.2</td>
</tr>
<tr>
<td>$\alpha_p$</td>
<td>Propensity for tail autotomy during predation</td>
<td>0.75-0.8</td>
</tr>
<tr>
<td>Variables</td>
<td>m</td>
<td>f</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>Mortality&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0.73</td>
<td>0.57</td>
</tr>
<tr>
<td>Tail loss frequency</td>
<td>0.68</td>
<td>0.53</td>
</tr>
<tr>
<td>Schoener’s index&lt;sup&gt;2&lt;/sup&gt;</td>
<td>1.23</td>
<td>0.89</td>
</tr>
<tr>
<td>Intensity of male-male combat&lt;sup&gt;3&lt;/sup&gt;</td>
<td>0.29</td>
<td>-</td>
</tr>
<tr>
<td>Food availability&lt;sup&gt;4&lt;/sup&gt;</td>
<td>0.94</td>
<td>2.82</td>
</tr>
<tr>
<td>Mean propensity for tail autotomy&lt;sup&gt;5&lt;/sup&gt;</td>
<td>0.283</td>
<td>0.173</td>
</tr>
</tbody>
</table>

<sup>1</sup> Deaths per 100 lizards per day

<sup>2</sup> Calculated using tail loss frequency in females

<sup>3</sup> Frequency of toe mutilation; not applicable in females

<sup>4</sup> Precipitation (in inches) during the activity season (March - August)

<sup>5</sup> Force (N) required to induce tail autotomy

Table 3.3: Parameter values of each population for predicting the optimal propensity
<table>
<thead>
<tr>
<th>Parameter</th>
<th>AZ</th>
<th>CA</th>
<th>NV</th>
<th>OR</th>
<th>WA</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P$</td>
<td>0.0065</td>
<td>0.0052</td>
<td>0.006</td>
<td>0.0056</td>
<td>0.0095</td>
</tr>
<tr>
<td>$f$</td>
<td>0.01</td>
<td>0</td>
<td>0.008</td>
<td>0</td>
<td>0.006</td>
</tr>
<tr>
<td>$S_f$</td>
<td>0.998</td>
<td>0.998</td>
<td>0.998</td>
<td>0.999</td>
<td>0.999</td>
</tr>
<tr>
<td>$c$</td>
<td>0.6</td>
<td>0.6</td>
<td>0.6</td>
<td>0.75</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Table 4.1: A summary of quantitative data on life-history related weight gain and locomotor impairment in animals.
APPENDIX B

FIGURES ASSOCIATED WITH EACH CHAPTER

64
Fig 1.1: The course of a jump made by a tailless green anole lizard. Note the extensive body rotation during the aerial phase and a high landing angle.
Fig 1.2: Comparisons of mean values for the first principal component (A and D), landing angle (B and E), and in-air body rotation (C and F) among the three groups of lizards: A–C, from data obtained in week 1; D–F, from week 5. Error bars represent standard errors. Within each figure, groups with the same letter did not differ significantly in post-hoc pairwise comparisons. N/A denotes overall lack of statistical significance in the ANOVA model.
Fig 1.3: Changes in the degree of in-air body rotation in all individuals during the study period. Each bar in the graph represents the same individual in week one, three and five. Note the extent of individual variation in two tailless groups. The asterisk denotes missing data for one individual in week five.
Fig 2.1: Bar plots comparing risk-taking behavior 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.
Fig 2.2: 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 denote 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.
Fig 3.1: A flow chart of the model illustrating all the events and the associated probabilities. The chart shows the first of 365 time steps. Note that some of the probabilities might change at later time steps.
Fig 3.2: The scaling relationship between $\alpha_b$ and $\alpha_p$ modeled using nonlinear increasing function.
Fig 3.3: Locations of the five *U. stansburiana* populations and habitat pictures. Shaded areas on the map denote range of distribution. The distribution map and the picture of *U. stansburiana* were obtained from Wikipedia Commons (commons.wikipedia.org). Habitat pictures were taken by C-YK.
Fig 3.4: Fitness curves (in blue) of different propensity values under low (A, B, C) and high (D, E, F) predation pressure and no (A, D; f = 0), medium (B, E; f = 0.005) and high (C, F; f = 0.01) male-male competition. Shaded areas represent 95% confidence interval. The number on the upper left corner of each plot is s values representing mean annual survival. The optimal propensities are the ones that confer the highest survival. An increase in predation only has an obvious effect on propensity under intense male-male combat, even though it significantly reduces survival (comparing graphs in the same column). On the other hand, the intensity of intrasexual competition has a more profound effect on optimal propensity. All graphs show results under high food availability.
Fig 3.5: Fitness curves of different propensity values under high (top panel) and low (bottom panel) food availability and low (A, C) and high (B, D) predation pressure. As in 3.3., the number above each plot denotes the mean annual survival $s$. 

![Fitness curves](image-url)
Fig 3.6: Model predictions (A, B) and field data (C, D) of the variation in the propensity for tail autotomy among five field *U. stansburiana* populations. The left two plots show the variation in males, and those on the right show that in females. The propensity values in c and d were the negative of force stimuli required to induce tail autotomy. Filled circles represent mean values for each population. The pattern of variation did not differ significantly between model prediction and field data in both sexes.
Fig 4.1: The modern ecomorphological paradigm highlighting the morphology-performance-fitness gradient and key factors that can affect this gradient, simplified from Lailvaux and Husak (2014). This review emphasizes the functional interactions between key life-history events and performance, depicted with red arrows. The red double arrows denote functional trade-offs between performance and two major life-history events, resource acquisition and reproductive investment. The red dotted arrows depict the roles of physiology and behavior in modulating the ecomorphological gradient.
Fig 4.2: Weight gain and the associated reduction in locomotor performance from 26 species. Circles, squares, and triangles represent speed, endurance and angle of ascent (only in birds). Open symbols denote terrestrial locomotion, shaded symbols aerial locomotion, and filled symbols aquatic locomotion. Data from the medicinal leach *Hirudo verbana*, which had 500% weight gain after feeding, was removed for the purpose of graphical presentation.
APPENDIX C

SUPPLEMENTAL FIGURES FOR CHAPTER III

Fig C.1: Fitness curves (in blue) of different propensity values under low (a, b, c) and high (d, e, f) predation pressure and no (a, d), medium (b, e) and high (c, f) male-male competition. Shaded areas represent 95% confidence interval. The results were simulated with $\alpha_b^p$ and $\alpha_b^p$ scaling linearly.
Fig C.2: Fitness curves of different propensity values under high (top panel) and low (bottom panel) food availability and low (a, c) and high (b, d) predation pressure. As in Figure S1, the results were obtained with $\alpha_b$ and $\alpha_p$ scaling linearly.
APPENDIX D

R-CODE FOR THE SIMULATION IN CHAPTER THREE

rm(list=ls())

#The function for generating data on days survived for one individual
AUTOTOMY<-function(Freq.fighting,Propensity) {

  OUTCOME.PREDATION<-c(2,1) #Sample vector for predator encounter; 2 means
  encountering a predator

  OUTCOME=c(1,0) #Sample vector for the occurrence of autotomy & survival; 1 means positive
  outcomes (autotomize/survive)

  survival<-1 #Survival at time = 0

  Time<-0 #Initialize time

  Pred.encoun<-0.0088#Predator encounter rate

  Cost.autotomy<-0.6#Scaling coefficient describing the decrease in baseline survival after
  autotomy; when =1, autotomy has no survival cost

  #Freq.fighting#Freq of male-male fightings

  Survival.baseline<-0.998#Baseline survival

  Time.max<-365#Number of total time steps

  #Time.max #Maximum time step over which the simulations are run

  #Freq.fighting #Frequency of male-male fighting

  #Propensity #Baseline propensity for autotomy

  Prob.auto.baseline<-Propensity*Freq.fighting #Baseline probability of autotomy

  Prob.auto.pred<-(10*Propensity/(1+10*9.5*Propensity))+0.7#Probability of autotomy during
  predation, its relationship with prop.baseline can be any non-decreasing function

  #Prob.auto.pred<-0.263*Propensity+0.74737#Modeling prop.baseline and probability during
  predation as a linear function instead

  #Survival.baseline #Baseline survival
Survival.auto <- Cost.autotomy * Survival.baseline # Survival after autotomy

RESULT <- matrix(0, Time.max, 4)

colnames(RESULT) <- c("Predator encounter", "Autotomize during predation", "Autotomize otherwise", "Survive")

while (Time < Time.max && survival == 1) { # bracket for while loop

  Time = Time + 1

  pred <- sample(OUTCOME.PREDATION, size = 1, prob = c(Pred.encoun, 1 - Pred.encoun), replace = T)

  if (pred == 2) {

    if (sum(RESULT[, 2:3], na.rm = T) <= 2) { # this means that a lizard can only autotomize up to 3 times

      auto.pred <- sample(OUTCOME, size = 1, prob = c(Prob.auto.pred, 1 - Prob.auto.pred), replace = T)

      auto.baseline <- NA

      if (auto.pred == 1) {

        survival <- sample(OUTCOME, size = 1, prob = c(Cost.autotomy * Survival.baseline, 1 - Cost.autotomy * Survival.baseline))

      } else {

        auto.pred <- NA

        auto.baseline <- NA

        survival <- 0

      }

    } else {survival <- 0}

  } else if (pred == 1) {

    if (sum(RESULT[, 2:3], na.rm = T) <= 2) {

      auto.pred <- sample(OUTCOME, size = 1, prob = c(Prob.auto.pred, 1 - Prob.auto.pred), replace = T)

      auto.baseline <- NA

      if (auto.pred == 1) {

        survival <- sample(OUTCOME, size = 1, prob = c(Cost.autotomy * Survival.baseline, 1 - Cost.autotomy * Survival.baseline))

      } else {survival <- 0}

    } else if (pred == 1) {

      if (sum(RESULT[, 2:3], na.rm = T) <= 2) {

      }

    }

  }

}
auto.pred<-NA

auto.baseline<-sample(OUTCOME,size=1,prob=c(Prob.auto.baseline,1-
Prob.auto.baseline),replace=T)

if (auto.baseline==1) {
    survival<-sample(OUTCOME,size=1,prob=c(Cost.autotomy*Survival.baseline,1-
    Cost.autotomy*Survival.baseline))
} else {
    survival<-sample(OUTCOME,size=1,prob=c(Survival.baseline,1-Survival.baseline))
}

} else {
    if (sum(RESULT[Time-30:Time,2:3],na.rm=T)==0) {#the cost of autotomy will persist up to
    30 days
        auto.baseline<-NA
        survival<-sample(OUTCOME,size=1,prob=c(Survival.baseline,1-Survival.baseline))
    } else {
        auto.baseline<-NA
        survival<-sample(OUTCOME,size=1,prob=c(Cost.autotomy*Survival.baseline,1-
        Cost.autotomy*Survival.baseline))
    }
}

RESULT[Time,]<-c(pred,auto.pred,auto.baseline,survival)

} #End of the while loop

days.survived<-sum(RESULT[,4])

return(days.survived)

}#End of the function AUTOTOMY

Nrep<-1000 #Number of simulations
LIFE.EXPECT<-rep(0,times=Nrep)
SURVIVAL.RATE <- rep(0, times = Nrep)

# Function generating data on mortality based on multiple individuals

FUNC.MORT <- function(P1, P2) {

  for (i in 1:1000) {
    LIFE.EXPECT[i] <- AUTOTOMY(Freq.fighting = P1, Propensity = P2)
    # head(LIFE.EXPECT)
    # summary(LIFE.EXPECT[,6])
    # hist(LIFE.EXPECT, breaks = 50, xlab = "# of days survived")
    LIFE.EXPECT.MEAN <- mean(LIFE.EXPECT)
    SURVIVAL.RATE <- sum(LIFE.EXPECT == 365) / 365
  } # the end of the i loop

  return(c(LIFE.EXPECT.MEAN, SURVIVAL.RATE))
  # return(SURVIVAL.RATE)
}

} # end of the function FUNC.MORT

# FUNC.MORT(P1 = 0.01, P2 = 0.2)

n1 <- 20; n2 <- 25

FIGHTING.SPACE <- c(0, 0.005, 0.01, 0.02)

PROP.SPACE <- seq(from = 0.01, to = 0.2, length = n2)

COMBINATION <- expand.grid(FIGHTING.SPACE, PROP.SPACE)

require(snowfall)

sfInit(parallel = T, cpus = 4)
LIFESPAN.VECTORE<-sfApply(COMBINATION,1,function(y){FUNC.MORT(P1 = y[1],P2 = y[2])})

#Output simulation results from 1000 iterations, to be used later
simulation<-cbind(COMBINATION,t(LIFESPAN.VECTORE))
colnames(simulation)<-c("Fight","Propensity","Day.survived","Survival.rate")
write.csv(simulation,"pred0.015_morefood.csv")

#LIFESPAN.MATRIX<-matrix(LIFESPAN.VECTORE,n1,n2)
#par(mfrow=c(1,1))
#persp(x=FIGHTING.SPACE,y=PROP.SPACE,z=LIFESPAN.MATRIX,theta=120,phi=15,xlab="Male-male fighting",ylab="Propensity",zlab="Survival (# of days)",main="Predator encounter rate = 0.05")
#contour(x=FIGHTING.SPACE,y=PROP.SPACE,z=LIFESPAN.MATRIX,xlab="MALE-MALE FIGHTING",ylab="PROPENSITY")

#par(mfrow=c(2,2))
#SIMULATION<-cbind(COMBINATION,LIFESPAN.VECTORE)
colnames(SIMULATION)<-c("Fighting","Propensity","Survival")
#plot(SIMULATION[SIMULATION$Fighting==0]$Propensity,SIMULATION[SIMULATION$Fighting==0]$Survival,type="l",xlab="Propensity",ylab="Survival",main="Male fighting = 0")
#plot(SIMULATION[SIMULATION$Fighting==0.005,]$Propensity,SIMULATION[SIMULATION$Fighting==0.005,]$Survival,type="l",xlab="Propensity",ylab="Survival",main="Male fighting = 0.005")

#plot(SIMULATION[SIMULATION$Fighting==0.01,]$Propensity,SIMULATION[SIMULATION$Fighting==0.01,]$Survival,type="l",xlab="Propensity",ylab="Survival",main="Male fighting = 0.01")

#plot(SIMULATION[SIMULATION$Fighting==0.05,]$Propensity,SIMULATION[SIMULATION$Fighting==0.05,]$Survival,type="l",xlab="Propensity",ylab="Survival",main="Male fighting = 0.05")

rm(list=ls())

#sim1<-read.csv("pred0.015lessfood_simulation1.csv")
#sim2<-read.csv("pred0.015lessfood_simulation2.csv")
#sim3<-read.csv("pred0.015lessfood_simulation3.csv")
#sim4<-read.csv("pred0.015lessfood_simulation4.csv")
#sim5<-read.csv("pred0.015lessfood_simulation5.csv")

#pred0.015lessfood<-rbind(sim1,sim2,sim3,sim4,sim5)
pred0.015morefood<-read.csv("pred0.015_morefood.csv")

fight0<-subset(pred0.015morefood,pred0.015morefood$Fight==0)
fight0.005<-subset(pred0.015morefood,pred0.015morefood$Fight==0.005)
fight0.01<-subset(pred0.015morefood,pred0.015morefood$Fight==0.01)
fight0.02<-subset(pred0.015morefood,pred0.015morefood$Fight==0.02)

fight0.plotdata<-aggregate(fight0$Day.survived,by=list(fight0$Propensity),FUN=mean)
colnames(fight0.plotdata)<-c("Propensity","Days survived")
write.csv(fight0.plotdata,"pred0.015morefood_fight0.csv")
fight0.005.plotdata<-aggregate(fight0.005$Day.survived,by=list(fight0.005$Propensity),FUN=mean)
colnames(fight0.005.plotdata)<-c("Propensity","Days.survived")
write.csv(fight0.005.plotdata,"pred0.015morefood_fight0.005.csv")

fight0.01.plotdata<-aggregate(fight0.01$Day.survived,by=list(fight0.01$Propensity),FUN=mean)
colnames(fight0.01.plotdata)<-c("Propensity","Days.survived")
write.csv(fight0.01.plotdata,"pred0.015morefood_fight0.01.csv")

fight0.02.plotdata<-aggregate(fight0.02$Day.survived,by=list(fight0.02$Propensity),FUN=mean)
colnames(fight0.02.plotdata)<-c("Propensity","Days.survived")
write.csv(fight0.02.plotdata,"pred0.015morefood_fight0.02.csv")


Davies, R.B. (1987) Hypothesis testing when a nuisance parameter is present only under the alternative. *Biometrika*, 74, 33–43.


