学位論文　（要約）

The functional morphology of locomotor system of anole lizards with different ecological habits

（異なる生息環境に適応したアノールトカゲ類の

運動器系における機能形態学的研究）

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Abstract

Understanding the functional relationships between morphological and ecological traits of vertebrates is one of the major goals of evolutionary biology. Especially the morphological characteristics of heads and limbs which are affected by locomotor behavior and habitat use are expected as important traits influencing the fitness. *Anolis* lizards have radiated adaptively and show highly diversity of species and morphological forms. In this thesis, I compared the locomotor system among species, sexes and populations of anoles and examined how morphological traits are related to behavior and habitat.

In the results of interspecies comparison, musculoskeletal systems of limbs show variation depending of microhabitat use. Terrestrial runner species possess larger mass of hindlimb extensors which is advantageous for running fast, whereas arboreal climbers are equipped with highly developed retractor which is adaptive to counteract gravity when climbing. Moreover the differences of forelimb muscles were indicated between arboreal active species and arboreal non-active species. The shorter moment arm producing wide excursion which is adaptive to branch-to-branch locomotion was observed in active species, whereas larger adductor muscles were shown in shoulder and elbow of non-active species which cling onto branch by whole arms and body. These findings suggest that divergent musculoskeletal characteristic in the limbs among *Anolis* species are strongly correlated with locomotor behavior and microhabitat use.

According to comparison of sexes, sexual dimorphisms were observed in forelimb muscles. In runner species which occur in terrestrial broad surface, male possess highly-developed humeral adductor which is adaptive to keep posture of display with expanding the dewlap. Larger extensor of elbow which is advantageous for display in narrow tree

substrates was observed in male of arboreal species which prefer arboreal habitat. These results indicate that significant sexual dimorphisms of appendicular musculoskeletal systems occur and the dimorphisms are related to habitat through the social display of male.

Also I compared the two populations of alien green anole in Ogasawara Islands, Japan. Male from Haha-jima showed larger body and larger heads, whereas male from Chichi-jima possessed relative wider and taller heads, however no differences of body and head size between islands were observed in females. I observed the male combat in laboratory and examined the relationships among morphological traits and success of the territorial combat by using Generalized Linear Mixed Model. As a result, the model with head width as explanatory variables was best fitting in Chichi-jima, whereas the model constructed by body size, head length and dewlap size was selected as most fitting theory in male of Haha-jima. These models indicate that relative wider head of male in Chichi-jima and larger body of male in Haha-jima are adaptive to success of territorial combat. Thus, it is suggested that the morphological differences between the two island populations have occurred only 30 years since isolation, and that the differences are affected by territorial combat between male individuals.

Finally, it is suggested that the locomotor systems of anole lizards have notably diversified among species, sexes and populations. In addition, the variated morphological traits are strongly affected by locomotor performance, habitat use and social behavior. The locomotor systems are considered as the evolutionarily important traits which relate functionally anole lizards to sympatric niche differentiation, speciation and diversification by both of natural and sexual selection.

Contents

Chapter 1.

General Introduction

One of the major goals of evolutionary biology is developing the theory why such great diversity in form and function has evolved (Futuyma, 1997). To achieve it, it is needed to understand the ecological and evolutionary consequences of organismal form. Tetrapods have diversified the taxa with various morphology and adapted to various habitat. Notably, morphology of locomotor system affect the fitness through the feeding, moving, fighting, mating or escaping in tetrapods. Locomotor styles of tetrapods, such as walking, running, jumping, climbing, flying or swimming are too diversified to compare the relationships between morphological traits and ecological traits among taxa. Hence, to explore the relationships among morphology, behavior and habitat, it is desirable to study closely related group included species with various morphological and ecological characteristics.

Anolis is one of the largest genera of lizards with over 400 species (Poe, 2004). The lizards show high rate of evolution, have radiated adaptively and show convergent evolution in form and habitat in the Caribbean Islands (Fig. 1-1; Losos, 2009; Losos et al., 1998; Nicholson et al., 2012). Different morphologies and behaviors have evolved in this genus, reflecting adaptation to differing micro-habitats (Losos et al., 1998). Furthermore, multiple species co-occurred sympatrically within a relatively small geographic area across the Greater Antilles, for instance, more than 10 species could be observed in same place in Cuba (Losos, 2009; Schettino et al., 2010). Hence, anoles have

been considered as model organisms for the study of adaptive radiation and correlations between ecology, behavior locomotion, and morphology.

The body size, body color, head form or limb length are varied adaptively to habitat environment ranging from ground to top of tree canopy among *Anolis* species (Williams, 1972; Beuttell and Losos, 1999). Focus on head shape, species using broad surfaces possess short, broad and high heads, whereas species that use narrow structures are equipped with long, slender and low heads (Harmon et al., 2005). It is considered that species occurred arboreal narrow substrates may need slender, low heads to maintain their balance and to enhance crypsis (Harmon et al., 2005; Losos, 2009). Not only head shape, but also head size affects bite force. In lizards, larger, shorter, higher and broader heads would be expected to bite harder, which could be useful in eating harder and larger prey or fighting with conspecifics (Schoener, 1968; Herrel et al., 2001; Verwaijen et al., 2002). Also the articles have reported correlations between the limb length and habitat or locomotor capacity. *Anolis* species with long hindlimb show high frequency of jump (Irschick and Losos, 1998; Toro et al., 2004) and tend to occupy high diameter of perch (Pounds, 1988). However, despite the fact that differences in musculoskeletal characteristics serve as a basis for diversification of locomotion and behavior, quantitative data are lacking on the force production mechanisms and appendicular musculoskeletal

morphology in this genus (Curtin et al., 2005). Although Vanhooydonck et al. (2006a, b) or Herrel et al. (2008) compared the muscular traits of limbs between various species, the major problems have remained with the theory, such as measuring together a plurality of muscles.

Intraspecific variation of morphological traits among populations are perceived as also interesting prediction for focusing on microevolutionary aspects of anole adaptation. Species ranged wide habitat often show geographical variations recognized as subspecies with different color pattern (Losos, 2009). Among Bahamian Islands, comparisons of population of *Anolis sagrei* and *Anolis carolinensis* revealed that a positive correlation exists between relative hindlimb length and diameter of used perch in both species (Losos et al., 1994). Alternatively, sexual dimorphisms have occurred in various species of anoles. Males are often substantially larger than females and fight with each other to maintain territories and access to the females, but in some species, females are larger (Fitch, 1976; Stamps, 1977). Relative length of limbs also shows difference between sexes (Butler et al., 2007). Then it remains unknown whether musculoskeletal systems show functional-morphological differences among populations or sexes and whether these intraspecific morphological variation is affected by differences of ecological habitat.

In this thesis, I report how the morphological characteristics of locomotor system are

functionally related to habitat environment, locomotor behavior and social behavior in wild *Anolis* lizards. In chapter 2, I examined the diversity of morphological characteristics in musculoskeletal systems of the appendicular region in Cuban species. Then the functional-morphological relationships among limb muscular traits, habitat use and locomotor behavior is revealed through the comparison among five species with different habitats. In chapter 3, I tested whether the sexual differences of musculoskeletal traits of limbs exist and whether the dimorphisms are affected by male specific social behavior with expanding the dewlap. In chapter 4, the intraspecific differences of morphological traits is explored in invasive green anole (*Anolis carolinensis*) between two island populations of Ogasawara Islands, Japan to verify what ecological traits affect the morphological differences which has occurred this 30 years. The aim of this thesis is to understand the functional-morphological base for access how *Anolis* lizards have speciated and diversified thorough the interspecific and intraspecific comparison with different locomotor habits.

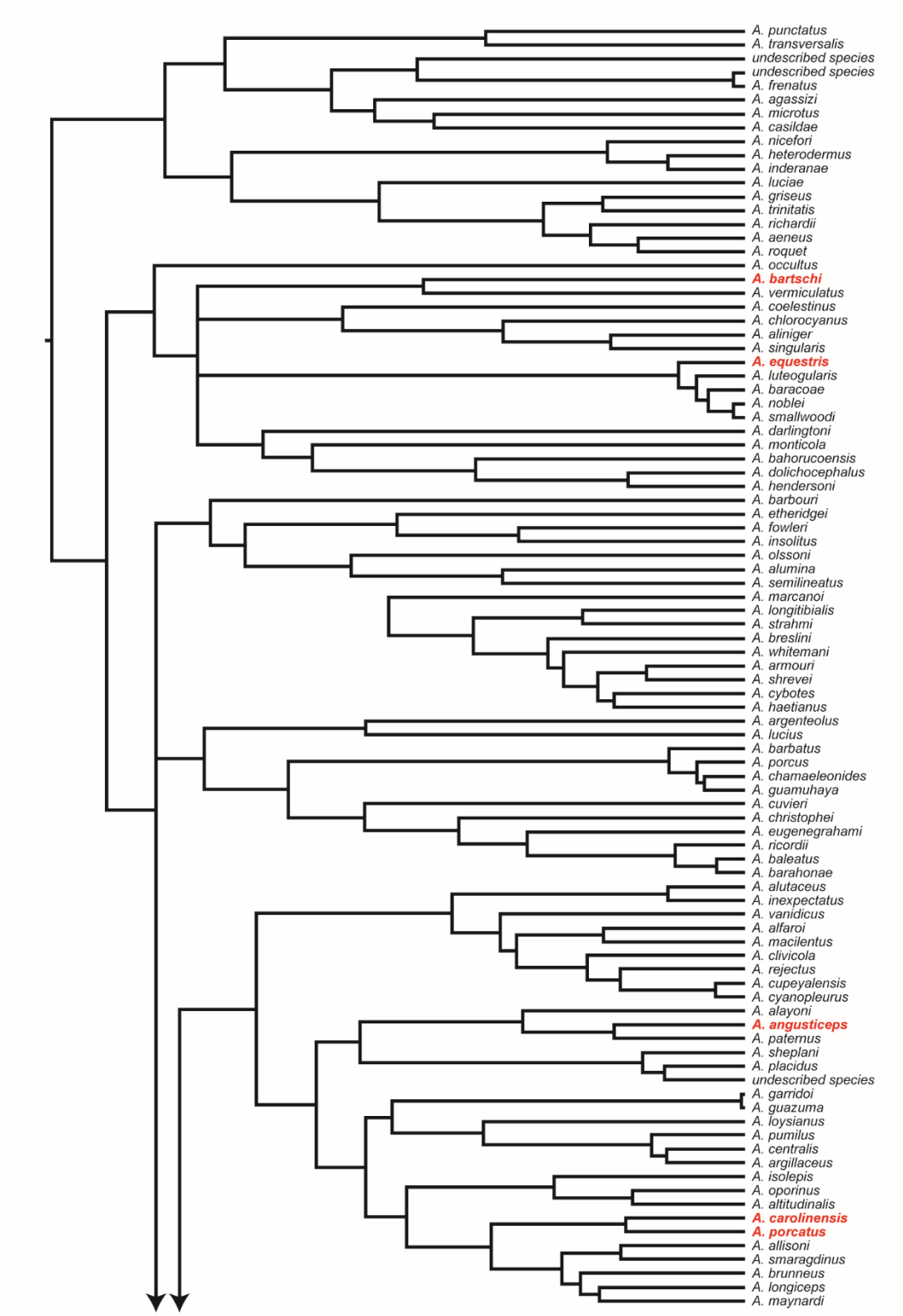

Figure 1-1. Phylogeny of 187 species of Caribbean anoles from Nicholson et al. (2005) and Losos (2009). The species which used in this thesis are indicated in red.

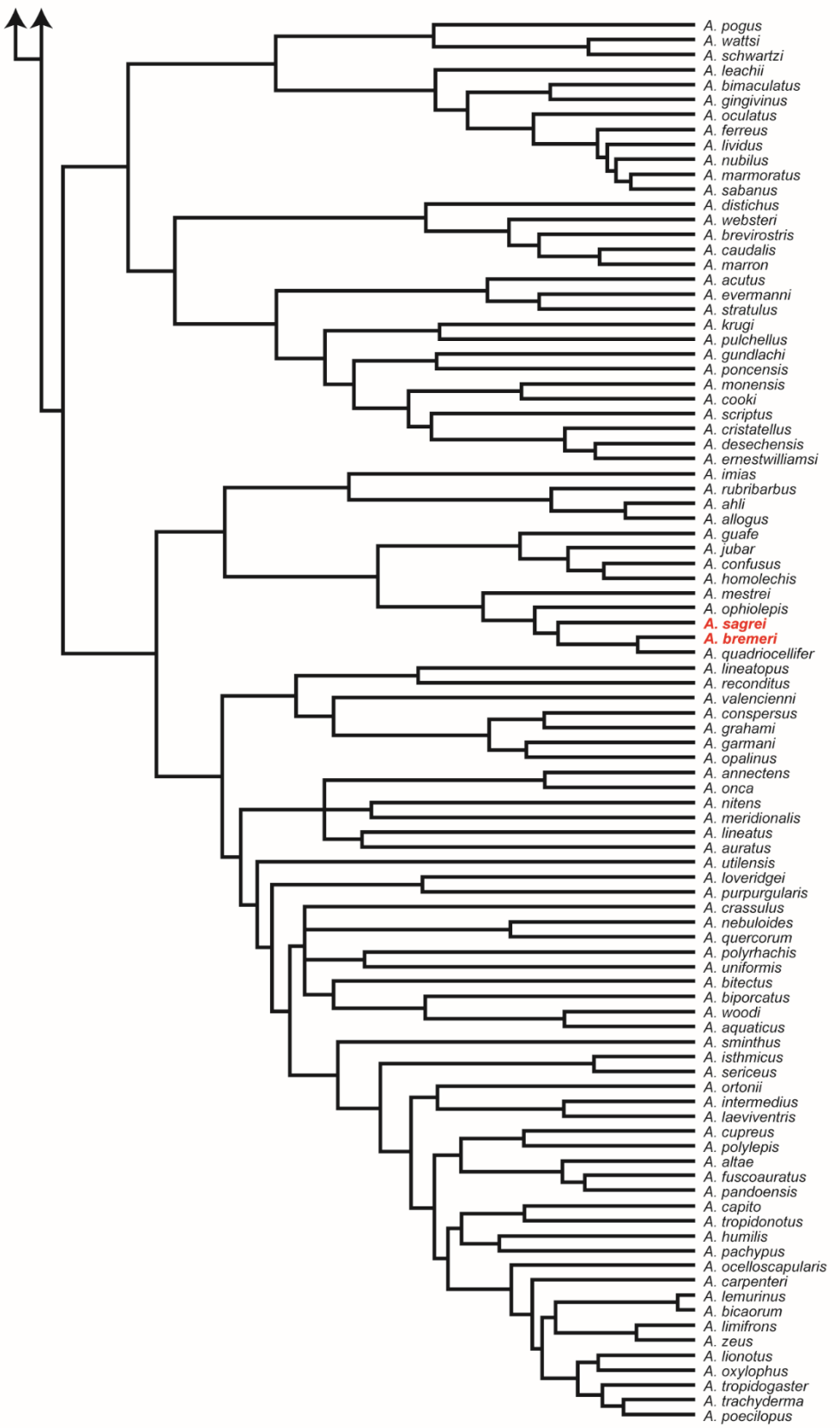

Figure 1-1 (continued).

Chapter 2.

Relationships among appendicular musculoskeletal morphology, locomotor behavior and habitat use in Cuban species

第２章

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This chapter is published as:

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Chapter 3.

Sexual dimorphisms of musculoskeletal traits of limbs and the effects of male specific social behavior in Cuban species

第３章

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Chapter 4

Morphological differences related male combat and micro-habitat between two island populations in Ogasawara Islands, Japan

第４章

本章については、５年以内に雑誌等で刊行予定のため、非公開。

Chapter 5.

General Discussion

Exploring the relationships between morphological traits and ecology

How has biodiversity been evolved? As mentioned in the introduction, to answer this question is the major goal of evolutionary biologists, and also the goal of this thesis. Various morphological differences between species are considered as the consequence of cumulative intraspecific differences pressured by the natural selection (Hendry and Kinnison, 2001). Are extant morphological variation between species and within species pressured by the same selection? If so, although the intraspecific polymorphism is considered as important factor to cause speciation, few experimental studies have examined the morphological evolution comprehensively from microevolution to macroevolution (Losos, 1994). This study is one of the challenge to the problem by exploring the relationships between morphological and ecological traits of *Anolis* lizards. And I could indicate the noticeable diversity of morphology in locomotor systems and the strong relationships among the morphological traits and ecological habits.

Variated musculoskeletal systems on limbs specialized for micro-habitat

As a result of comparison between species and sexes, it is indicated that appendicular musculatures of *Anolis* have diversified in closely related taxa. Besides, the morphological differences reflected strongly the habitat use and locomotor behaviors.

Especially discrimination between terrestrial or arboreal habitats related to the limbs well, hindlimb extensors, which are advantageous for running, are enlarged in terrestrial species, whereas arboreal species possess highly developed retractor muscles for humerus and femurs. Also both male and female show commonly the relationships. Muscular differences were observed in forelimb of arboreal lizards among active species and cryptic species. In *Anolis*, more than ten species occur sympatrically in micro-habitats isolated by arboreal substrates (Williams, 1972; Schettino et al., 2010). And it is interesting question why the species richness can exist in the restricted area (Cádiz et al., 2013). Since the variation of musculoskeletal systems revealed in this study are strongly specialized for the microhabitat, the morphological traits are considered as a factor for microscopic niche differentiation in *Anolis*.

Also in intraspecific comparisons, the differences of appendicular muscular traits were shown between two island populations of green anoles. Because of the different vegetation (Shimizu, 1994; 1999) and substrate types demonstrated between populations, it is probable that the habitat use affects muscular systems on limbs in Ogasawara Islands. Although no remarkable differences observed between terrestrial/arboreal species were presented, distinguishable muscular traits may be related to perch diameter or angle were indicated between two island populations. It is considered that the morphological

differences between populations have been evolved only in a few decades under the selection with different microhabitats. It is suggested that these specialization for various habitats on appendicular musculoskeletal systems have a potential for niche differentiation and sympatrically speciation.

The sexual dimorphisms of locomotor systems related to social behavior

In this study, sexual dimorphisms were distinguished in appendicular musculoskeletal traits, as indicated in body size or relative limb length (Schoener, 1969; Butler et al., 2007). Notably sexual differences in muscles of forelimb have a potential for being affected by postures when male is displaying. Although studies using *Anolis* have been focused on the display with dewlap, no theory has been explained about the relationships among morphological traits, such as size, color or pattern, behavioral traits of display and habitat environments (Losos and Chu, 1998; Nicholson et al., 2007). In this study, I suggest the possibility that display with dewlap may be affected by microhabitat, through the posture of display and the sexual dimorphisms of musculoskeletal systems in forelimb. If this hypothesize is true, the morphological differences in the forelimb muscles or the distinguished posture during the display would be observed in *Anolis* species occurring in adjacent habitat. It is indicated that the appendicular musculoskeletal systems have

been pressured not only by natural selection, but also by sexual selection through the social display and the evolution rate have been accelerated in *Anolis* lizards.

Also I indicated the relationships between intraspecific differences among male body size, head form and male combat in alien green anole. The morphological differences in male seemed to be affected by the selection to attain efficiently the territory and partner of mating at the novel habitat environment. The previous studies showed predominant sexual dimorphism of anoles from islands within an *Anolis* species instead of the sympatric speciation (Schoener, 1977; Losos, 2004). It is consistent with my results which indicated that the sex-depending differences of locomotor systems between islands occurred in the young populations in only 30 years since isolation. Moreover, since habitat type differed according to sex, sexual dimorphisms in locomotor systems may be affected by different habitat use between male and female. For active male, it may be important to obtain the locomotor systems which is adaptive to move and ensure the mating chance, whereas adapting to tree substrate by suited form of limbs may have priority for cryptic female.

Thus social behavior seen in male specifically and locomotor habits depending on the sex are considered to have strong effects on speciation and diversification. And this study indicated that the sexual dimorphisms of locomotor systems are obviously reflected in the

effects.

Unstoppable evolution of anole lizards

In Lesser Antillean, the islands contain at most two species, and no relationship exists between area of island and number of species (Schoener, 1970). In the islands with only one species, arboreal, active and medium size lizard, like green anole, is distributed routinely (Schoener, 1970; Losos and Queiroz, 1997). Whereas character displacement occurred in islands with two species, the islands contain a large species perching higher and a small species prefers lower perch (Schoener, 1970; Roughgarden, 1995; Losos, 2009). Although it has remained unknown why first species is arboreal and medium-sized, the populations from these islands are considered to be in earlier stages for diversification of *Anolis* species (Lazell, 1972; Losos, 2009).

It is suggested that also green anole in Ogasawara Islands have a potential for speciation. Although poorly genetic variation by bottle neck effects is observed, distribution of *A. carolinensis* has been ranged by highly moving capacity and omnivorous feeding habits in Chichi-jima and Haha-jima (Hasegawa, 1988; Hayashi, 2009a; Sugawara et al., 2015). In addition, this study presents that microevolution has occurred between island populations for only 30 years. The lizards are interesting model organisms for

evolutionary biology, however are also troubling enemies for preservation of environment. Studying morphological and ecological evolution of anole is fruitful for both development of the evolutionary theory and conservation of the natural environment. Furthermore, *A. carolinensis* became the first non-avian reptiles that the whole-genome is sequenced (Alföldi et al., 2011), and the advancement of genomics analyses is expected in this species. When it will be developed, or along with it, cumulative experiments of phenotype must help and deepen the understanding of the evolution of anoles. It is considered that classical methods used in this study, such as comparing the morphological systems, observations of behavior and measurements of habitat, will continue to develop the evolutionary biology both now and in the future.

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