
Learning the locomotion behaviour of lizards transfers across environments

Kathleen Lois Foster ^{*1}
Alessandro Maria Selvitella ^{*2}

Abstract

Successful locomotion is essential for the survival of most animals and crucial for arboreal species. In this paper, we analyze the locomotor behaviour of a species of lizard, *Anolis carolinensis*, from the perspective of transfer learning. By analyzing the limb movements of 4 individuals on 6 different surfaces (3 inclinations \times 2 perch diameters), we show that the strategies employed to improve stability during locomotion on narrow perches can be transferred across environments with different inclines. This transfer of behaviour is analogous to phenotypic plasticity, which likely plays a key role in the rapid adaptive evolution characteristic of *Anolis* lizards. This novel result emphasizes the valuable contribution that modern machine learning perspectives can give to the study of comparative biomechanics.

1. Introduction

Anolis lizards are a model system for a number of facets of biology and are especially important for evolutionary studies (Poe et al., 2017; 2018; Román-Palacios et al., 2018). In particular, *Anolis* lizards are noted for the rapid and repeated evolution of ecomorphs, species whose morphology, behaviour, and ecology have evolved concordantly to enable them to specialize for particular arboreal microhabitats (Losos, 1990a;b; 2009). This adaptation occurs in response to exposure to new niches, (e.g. occurring because of dispersal to new islands) and in response to competitive displacement (Losos et al., 1997). For example, it has been shown that *Anolis carolinensis* quickly adapted its locomotor behaviour and morphology to new environments in response to the introduction of an invasive species of anole, *A. sagrei* (Stuart et al., 2014). *A. carolinensis* was relegated to higher

perches and, in response, evolved to accommodate the new habitat after only 20 generations (Stuart et al., 2014).

Possibly due to the importance of the genus for evolutionary biology, *A. carolinensis* was chosen as one of the first reptilian species for genome sequencing (Modi & Crews, 2005; Rovastos et al., 2015; Alföldi et al., 2011). *A. carolinensis* is a small lizard common to the South-East of the United States. As an arboreal generalist, *A. carolinensis* is found on a variety of substrates ranging from the top-most, narrow branches of trees, to broad vertical tree trunks, to the ground (Mattingly & Jayne, 2004; Irschick et al., 2005a;b). Because of this generalist behaviour, *A. carolinensis* encounters surfaces that vary dramatically in incline, perch diameter and complexity, which not only impose functional challenges for the animal, but raises interest questions about the morphological, biomechanical, and physiological strategies needed for survival in such a heterogeneous environment.

Due to the complexity of the phenomenon under study, which is at the interaction of biology and physics, and the lack of satisfactory mathematical modeling of the full body dynamics of lizards, most studies in biomechanics and of *A. carolinensis* in particular, are partial and confined to traditional statistical methods, in order to at least satisfy biological interpretability requirements (Foster & Higham, 2012; 2014; Mattingly & Jayne, 2004). While physiological branches of biology, like biomechanics, seem to be stuck in the past, with the ubiquitous and almost exclusive use of classical univariate statistics, advancements in computing power have facilitated the development and application of sophisticated methods to biological fields such as genomics, ecology, and evolution.

In this work, we study the locomotor behaviour of *A. carolinensis*, using the modern machine learning perspective of generalization, but restricting our analysis to interpretable algorithms, and show how this point of view can provide a deeper insight to fundamental questions in biology, such as the fast adaptability of certain reptiles to new environments. We focus on understanding the locomotor behaviour of *A. carolinensis*, and showing how biologically meaningful features of the dynamics of this species on heterogeneous habitats transfer across environments (3 inclinations - 0, 45, 90 - deg \times 2 perch diameters - broad, narrow -). Previous studies have taken a descriptive approach and found that limb movements and function of the forelimbs and hind limbs shift on different arboreal substrates to increase stability, particularly on narrow substrates (Foster & Higham,

^{*}Equal contribution ¹Department of Biology, Ball State University, Muncie IN, USA ²Department of Mathematical Sciences, Purdue University Fort Wayne IN, USA. Correspondence to: Kathleen Lois Foster <klfoster@bsu.edu>, Alessandro Maria Selvitella <aselvite@pfw.edu>.

2012; 2014). Our analysis builds on these results by using *Transfer Learning* (TL) related ideas and *Linear Discriminant Analysis* (LDA) to understand how common locomotor strategies can facilitate movement on different substrates. We will not leverage our analysis to the most advanced non-linear algorithms, since the negligible and not biologically significant improvement in accuracy will come with loss of interpretability of the results. Interestingly, we show that the features that transfer across heterogeneous environments are the ones relevant to stability and enable the accurate prediction of perch diameter on any of the inclines tested. This result gives a new perspective to the understanding of the adaptability of *A. carolinensis*'s functional morphology across environments, and gives a biologically meaningful explanation of which factors contribute to this adaptability.

The remaining part of the paper is organized as follows. In Section 2, we describe the experiments and the datasets; In Section 3 we describe the algorithms used; In Section 4, we present and discuss our results; In Section 5, we summarize our results and give our conclusions.

2. Experiments and Datasets

The data for this study were obtained from (Foster & Higham, 2012). As the experimental methods are described in detail there, we will only outline the setup as it relates to the structure of our dataset. Briefly, four adult *A. carolinensis* (Fig. 1) were filmed at 500 frames/sec with two high speed video cameras while running on 1m long broad (9 cm wide) or narrow (1.3 cm diameter) perches inclined at 0 deg, 45 deg, and 90 deg. For each condition, 2-5 strides were selected for analysis if both limbs were visible and the lizard ran steadily on the top of the perch through the entire field of view.



Figure 1. Photo of *Anolis carolinensis*. Photo credit: KLF.

For all videos selected for analysis, 13 landmarks on the lizards bodies were digitized and used to calculate the variables to capture position and movement of the body (body speed, and pectoral/pelvic girdle rotation and height above

the perch surface) and limbs (duty factor, stride frequency, and 3D joint angles and angular velocities). See (Foster & Higham, 2012) for further details. To incorporate how each of these variables changed during the course of the stride, values x_t that corresponded to biologically meaningful time points (e.g. beginning or end of the period of foot-surface interaction - stance phase -) were extracted from the time series y_t of each landmark. The final dataset consists of 38 variables for each limb for a total of 74 variables, after 2 duplicate variables (body speed and stride frequency) were removed. A total of 76 strides were analyzed for the forelimb and 89 strides for the hind limb.

For the analysis, the full dataset was divided in 9 different subsets. First in 3 groups by limb (forelimb only, hind limb only, and both limbs combined), and then each of them was further divided in 3 by variable type (angular variables, angular velocity variables, and angular+angular velocity variables combined; see Table 1). This subdivision was made to test environment-knowledge transfer across habitats in as many cases as our data allowed.

3. Methods

This section briefly explains TL and LDA.

Transfer Learning

TL is at the core of machine intelligence and concerns how algorithms trained to perform a task can perform well on a different task (Pratt, 1993; Goodfellow et al., 2017). In its essence, TL is motivated by the question of understanding how animals transfer and acquire knowledge much quicker than machines.

Suppose each of the landmark observations for the locomotion of lizards on a specific environment \mathcal{E} live in a space \mathcal{X} and are distributed with pdf $f_{\mathcal{X}}(x)$. Suppose that an algorithm is trained to learn \mathcal{E} from \mathcal{X} , using a sample $\{x_i, e_i\}_{i=1}^n \in \mathcal{X} \times \mathcal{E}$. This procedure outputs a prediction rule $f : \mathcal{X} \rightarrow \mathcal{E}$. TL aims at transferring the biological features learned in this task to a new environment, and thus to a new feature space \mathcal{X}' , novel labels \mathcal{E}' , and possibly a different learning rule f' , derived from a new set of observations $\{x'_i, e'_i\}_{i=1}^{n'} \in \mathcal{X}' \times \mathcal{E}'$. In our case, we will concentrate on what is called *zero-shot learning* or *zero-data learning* (Larochelle et al., 2008; Palatucci et al., 2009; Socher et al., 2013), namely the case in which no information about the classes in the test phase is provided during training.

Linear Discriminant Analysis

LDA is a classification algorithm, which relies on the application of the Bayes rule to assign a label to a specific set of variates (James et al., 2013).

Suppose we want to classify a multivariate time series of landmarks representing the locomotion of one specimen

into one of K classes. The prior probability of belonging to one of the classes is independent of the class. Define $f_k(y_t) = P(Y = y_t | C = k) = P(X = x_t | C = k)$ the probability distribution of a time series y_t from class k . In our analysis we use a single specific calculated measurement x_t from the time series y_t (e.g. beginning or end of the period of foot-surface interaction - stance phase -). Using Bayes theorem and imposing equally probable classes, we have:

$$P(C = k | Y = y_t) = \frac{f_k(y_t)}{\sum_{k=1}^K f_k(y_t)}.$$

Moreover, suppose that $f_k(y_t) \sim MVN(\mu_k, \Sigma)$, then the Bayes classifiers assigns the time-series to the class c such that

$$c = \arg \max_{k=1, \dots, K} B_k(y_t),$$

with

$$B_k(y_t) = 2x_t' \hat{\Sigma}^{-1} \hat{\mu}_k - \hat{\mu}_k' \hat{\Sigma}^{-1} \hat{\mu}_k,$$

and where $\hat{\mu}_k$ and $\hat{\Sigma}$ are the class sample mean and the sample variance-covariance matrix of the x_t 's, respectively, and can depend on which biologically meaningful x_t is extracted from the time series. This method is called LDA, since the discrimination rule is a linear function of x_t .

Training and Testing

The training and testing folds used in our analysis do not contain common class environments. For example, we train a model to distinguish between perch diameters using only time series coming from the dynamics on a single inclination, and then we test its classification performance on the remaining two inclinations. This case is in fact more complicated than training instead on two inclinations and testing on one, or providing all class environments both in the training and testing phase. We refer to Table 1 for the full set of models analyzed.

4. Results and Discussion

This section is dedicated to the results of our analysis and their importance for the biomechanics of lizards.

Successful TL is substrate and limb/input specific

Successful TL (prediction accuracy > 0.80) was achieved in LDA models trained to distinguish between perch diameters given a single incline, and tested on the remaining two inclinations (Fig. 2). LDA fails to distinguish between inclines when tested on unseen perch diameters. The inclines which better transfer information to the others depend on which features (forelimb, hind limb, or both; angles, angular velocities, or both) are provided as input to the algorithm. Given forelimb angular data, only training with the 90 deg incline enabled the model to successfully predict perch diameter in the remaining two inclines (0.91 accuracy; Table 1). In contrast, no model could successfully generalize when using forelimb angular velocity data, whereas when using the

Table 1. In this table we report the results of our experiments on the different prediction tasks we analyzed. We used the following abbreviations: FL=forelimb, HL=hind limb, BL=both limbs; ang.=angular variables, vel.=angular velocity variables, all=angular+angular velocity variables, 0=level, 45=45 degree incline, 90=90 degree incline, diam.=diameter, incl.=incline.

VARIABLES	TRAIN	TEST	TASK	ACCURACY
FL - ANG.	0	45,90	DIAM.	0.38
FL - ANG.	45	0,90	DIAM.	0.65
FL - ANG.	90	0,45	DIAM.	0.91
FL - ANG.	BROAD	NARROW	INCL.	0.44
FL - ANG.	NARROW	BROAD	INCL.	0.52
FL - VEL.	0	45,90	DIAM.	0.60
FL - VEL.	45	0,90	DIAM.	0.60
FL - VEL.	90	0,45	DIAM.	0.57
FL - VEL.	BROAD	NARROW	INCL.	0.51
FL - VEL.	NARROW	BROAD	INCL.	0.73
FL - ALL	0	45,90	DIAM.	0.81
FL - ALL	45	0,90	DIAM.	0.81
FL - ALL	90	0,45	DIAM.	0.70
FL - ALL	BROAD	NARROW	INCL.	0.47
FL - ALL	NARROW	BROAD	INCL.	0.45
HL - ANG.	0	45,90	DIAM.	0.91
HL - ANG.	45	0,90	DIAM.	0.85
HL - ANG.	90	0,45	DIAM.	0.89
HL - ANG.	BROAD	NARROW	INCL.	0.29
HL - ANG.	NARROW	BROAD	INCL.	0.45
HL - VEL.	0	45,90	DIAM.	0.89
HL - VEL.	45	0,90	DIAM.	0.85
HL - VEL.	90	0,45	DIAM.	0.69
HL - VEL.	BROAD	NARROW	INCL.	0.69
HL - VEL.	NARROW	BROAD	INCL.	0.40
HL - ALL	0	45,90	DIAM.	0.89
HL - ALL	45	0,90	DIAM.	0.85
HL - ALL	90	0,45	DIAM.	0.82
HL - ALL	BROAD	NARROW	INCL.	0.31
HL - ALL	NARROW	BROAD	INCL.	0.30
BL - ANG.	0	45,90	DIAM.	0.81
BL - ANG.	45	0,90	DIAM.	0.79
BL - ANG.	90	0,45	DIAM.	0.87
BL - ANG.	BROAD	NARROW	INCL.	0.44
BL - ANG.	NARROW	BROAD	INCL.	0.61
BL - VEL.	0	45,90	DIAM.	0.43
BL - VEL.	45	0,90	DIAM.	0.56
BL - VEL.	90	0,45	DIAM.	0.66
BL - VEL.	BROAD	NARROW	INCL.	0.70
BL - VEL.	NARROW	BROAD	INCL.	0.67
BL - ALL	0	45,90	DIAM.	0.94
BL - ALL	45	0,90	DIAM.	0.75
BL - ALL	90	0,45	DIAM.	0.89
BL - ALL	BROAD	NARROW	INCL.	0.35
BL - ALL	NARROW	BROAD	INCL.	0.45

entire forelimb dataset, models trained on 0 deg and 45 deg inclines both were successful at generalizing to perch diameters in the remaining two inclines (0.81 accuracy; Table 1). In the hind limb, when given both angular variables alone and the entire hind limb dataset, any inclination could be used to successfully predict perch diameter in the remaining two inclinations (0.82-0.91 accuracy; Table 1) whereas only the 0 deg and 45 deg inclines could be used to train successful models when given only hind limb angular velocity data. Finally, when data from both limbs were combined, models trained on 0 deg and 90 deg, but not 45 deg, were able to generalize well to the remaining inclines, but only when using angular data only or a combination of angular and angular velocity data (0.81-0.94 accuracy; Table 1).

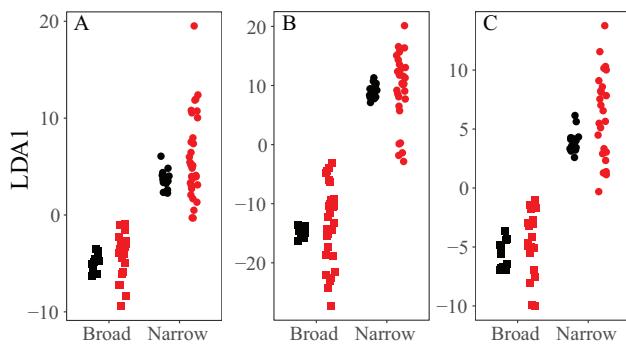


Figure 2. Plots of LDA scores for training (black) and test (red) sets, separated by perch diameter (squares=broad, circles=narrow). Plots shown are for the best models: A) trained on 90 deg with the forelimb angular variables (prediction accuracy= 0.91), B) trained on 0 deg with the hind limb angular variables (prediction accuracy=0.91, C) trained on 0 deg with the complete dataset (prediction accuracy=0.94).

Features transferring across environments

In order to understand which biologically meaningful variables contributed most strongly to the models that are successfully able to transfer the learning of perch diameter to different inclines, we correlated our input variables against the corresponding LDA classification hyperplanes. The forelimb variables used to create models with the highest accuracy of TL were shoulder height (lower on narrow vs broad perch), humerus depression, rotation, and retraction (greater on narrow vs broad perch), elbow flexion (greater on narrow vs broad perch), duty factor (higher on narrow vs broad perch), and humerus depression, rotation, and retraction velocity during swing phase (faster on narrow vs broad perch). Similarly, the hind limb variables used to create the best TL models were hip height (lower and more stable on narrow vs broad perch), femur depression and retraction, and knee and ankle flexion (greater, and moved over greater range of angles on narrow vs broad perch), femur rotation (less, and moved over smaller range of angles on narrow

vs broad perch), pelvic girdle rotation (less on narrow vs broad perch), body speed (slower on narrow vs broad perch), and swing and stance phase velocities of femur retraction, rotation, knee, and ankle angles (faster on narrow vs broad perch). In models that included both forelimb and hind limb data, the majority (> 75%) of variables that correlated strongly (> 0.7) belonged to the hind limb. Even among variables that correlated > 0.5, > 62% belonged to the hind limb.

Evolutionary implications of TL in *Anolis* lizards

As explained above, the variables that transfer across environments (inclinations) are the ones that are integral to lowering the center of mass, flexing the limbs, and wrapping limbs around on the sides of narrow perches. These traits are all consistent with known strategies for improving stability on narrow substrates (Foster & Higham, 2012). This is further supported by the fact that the variables that appear to transfer across environments in the majority of our best models relate to the hind limb, which has been suggested to take on a more stabilizing role on narrow surfaces (Foster & Higham, 2012). The principles underlying TL and the results of our analysis connect to the rapid adaptive radiation, likely facilitated by plasticity (West-Eberhard, 1989; Losos et al., 2000; Kolbe & Losos, 2005), that has made *Anolis* lizards a model system in biology. If pre-existing behaviours that facilitate locomotion on narrow surfaces are useful on multiple types of inclines, then the locomotor plasticity manifested through the transfer of the traits that facilitate locomotion on those surfaces should give an adaptive advantage by improving stability of motion and indeed, survival in those new complex environments.

5. Conclusions

In this work, we have leveraged machine learning methods, specifically TL, to gain insights into the functional demands on locomotion imposed by the arboreal environment. Our results demonstrate that it is possible to learn to identify the diameter of the surface that our anoles are running on, regardless of the inclination of the surface and that this TL capability is limb-specific. Further, we show that the variables integral to this TL process are the ones that relate to locomotor stability. Locomotor stability is a crucial factor for the survival of arboreal species, and the ability of *A. carolinensis* to adapt locomotor behaviour might reflect the evolutionary advantage of having limbs functioning in complex habitats and being able to transfer skills across heterogeneous environments for the sake of survival. Of fundamental importance is to test how our models generalize to different species of lizards as this could provide insights into the plasticity and adaptability of reptiles.

References

- Alfoldi, J., Palma, F. D., Grabherr, M., and et al. The genome of the green anole lizard and a comparative analysis with birds and mammals. *Nature*, 477(7366):587–591, 2011.
- Foster, K. and Higham, T. How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis*. *Journal of Experimental Biology*, 215:2288–2300, 2012.
- Foster, K. L. and Higham, T. E. Context-dependent changes in motor control and kinematics during locomotion: modulation and decoupling. *Proceedings of the Royal Society of London B: Biological Sciences*, 281:20133331, 2014.
- Goodfellow, I., Bengio, Y., and Courville, A. *Deep Learning*. MIT Press, 2017.
- Irschick, D. J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B., Meyers, J. A. Y., and Herrel, A. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society*, 85:223–234, 2005a.
- Irschick, D. J., Vanhooydonck, B., Herrel, A., and Meyers, J. A. Y. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biological Journal of the Linnean Society*, 85:211–221, 2005b.
- James, G., Witten, D., Tastie, T., and Tibshirani, R. *Introduction to Statistical Learning*. Springer, 2013.
- Kolbe, J. J. and Losos, J. B. Hind-limb length plasticity in *Anolis carolinensis*. *Journal of Herpetology*, 39:674–678, 2005.
- Larochelle, H., Erhan, D., and Bengio, Y. Zero-data learning of new tasks. In *Proceedings of the Twenty-Third AAAI Conference on Artificial Intelligence*, pp. 646–651, 2008.
- Losos, J. B. The evolution of form and function: morphology and locomotor performance in west indian *Anolis* lizards. *Evolution*, 44:1189–1203, 1990a.
- Losos, J. B. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Animal Behaviour*, 39:879–890, 1990b.
- Losos, J. B. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, 2009.
- Losos, J. B., Warheit, K. I., and Schoener, T. W. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, 387:70–73, 1997.
- Losos, J. B., Creer, D. A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., Haskell, N., Taylor, P., and Ettling, J. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution*, 54: 301–305, 2000.
- Mattingly, B. W. and Jayne, B. C. Resource use in arboreal habitats: structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, 85:1111–1124, 2004.
- Modi, W. and Crews, D. Sex chromosomes and sex determination in reptiles. *Curr Opin Genet Dev*, 15:660–665, 2005.
- Palatucci, M., Pomerleau, D., Hinton, G. E., and Mitchell, T. M. Zero-shot learning with semantic output codes. In Bengio, Y., Schuurmans, D., Lafferty, J., Williams, C., and Culotta, A. (eds.), *Advances in Neural Information Processing Systems 22*, pp. 1410–1418, 2009.
- Poe, S., de Oca, A. N.-M., Torres-Carvajal, O., Queiroz, K. D., Velasco, J. A., Truett, B., Gray, L. N., Ryan, M. J., Köhler, G., Ayala-Varela, F., and Latella, I. A phylogenetic, biogeographic, and taxonomic study of all extant species of anolis (squamata; iguanidae). *Syst. Biol.*, 66 (5):663–697, 2017.
- Poe, S., de Oca, A. N.-M., Torres-Carvajal, O., Queiroz, K. D., Velasco, J. A., Truett, B., Gray, L. N., Ryan, M. J., Köhler, G., Ayala-Varela, F., and Latella, I. Comparative evolution of an archetypal adaptive radiation: Innovation and opportunity in anolis lizards. *The American Naturalist*, 191(6):E185–E194, 2018.
- Pratt, L. Discriminability-based transfer between neural networks. *NIPS Conference: Advances in Neural Information Processing Systems*, 5:204–211, 1993.
- Román-Palacios, C., Tavera, J., and del R. Castañeda, M. When did anoles diverge? an analysis of multiple dating strategies. *Molecular Phylogenetics and Evolution*, 127: 655–668, 2018.
- Rovastos, M., Vukić, J., Lymberakis, P., and Kratochvíl, L. Evolutionary stability of sex chromosomes in snakes. *Proc. R. Soc. B*, pp. 20151992, 2015.
- Socher, R., Ganjoo, M., Manning, C. D., and Ng, A. Y. Zero-shot learning through cross-modal transfer. *Advances in Neural Information Processing Systems 27*, 2013.
- Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., and Losos, J. B. Rapid evolution of a native species following invasion by a congener. *Science*, 346(6208):463–466, 2014.
- West-Eberhard, M. J. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, 20:249–278, 1989.