

Pirates of the Caribbean (and Elsewhere): Three-Legged Lizards and the Study of Evolutionary Adaptation

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ABSTRACT: Natural selection is widely considered responsible for the fit between organisms and their environment. Lizard limb length variation is a paradigmatic example: studies have shown that limb length differences tightly correlate with habitat use among species, while small differences in limb length between individuals can affect biomechanical function, fitness, and survival within populations. It has therefore been surprising for many field biologists to find otherwise-healthy wild lizards with damaged or missing limbs, appearing to challenge associated expectations of substantial fitness costs. We document limb loss (from a foot to an entire limb) in 58 lizard species, with all cases showing healed limbs and many lizards appearing robust and healthy. Data indicate that limb-deficient lizards typically comprise less than 1% of populations and often exhibit body condition, sprint speed performance, and survival comparable to limb-intact individuals. We discuss the implications of these findings for how evolutionary adaptation is studied and understood in natural populations and provide a perspective on conventional assumptions about the strength and ubiquity of selection pressures on seemingly critical traits. Is natural selection always as omnipresent as Darwin envisioned it to be?

Keywords: natural selection, adaptation, adaptive evolution, limb loss, fitness.

It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, wherever and whenever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. (Darwin 1859)

Introduction

Although Darwin's view may be considered an extreme perspective by some, many—perhaps most—biologists consider species to be locally adapted to the environment in which they live. A key implication of this perspective is that individuals with major deformities in functionally important traits should be at a substantial disadvantage (Hendry et al. 2022); such individuals would not be expected to survive very long and thus rarely be present in natural populations.

The genesis of this article was an incident involving the senior author (J. B. Losos) during a study of natural selection on island populations of the brown anole, *Anolis sagrei*, in the Bahamas (Losos et al. 2004, 2006). In the preceding year, all individuals on each island had been captured, measured, marked, and released. During a recapture session, Losos battled a wily lizard that was nimbly locomoting over the narrow branches, evading capture. Only when the lizard was finally in hand did he realize that it was missing its entire left hind leg. A year previous, when the lizard had initially been captured and marked, it had the typical complement of four legs. In the elapsed year, the limb had been

lost, the wound healed, and the animal was fat and sassy, seemingly no worse for the trauma. Although surprised by the episode, the senior author did not give it much thought. However, over the years he occasionally encountered additional seemingly healthy lizards missing part or all of a limb. Conversations with colleagues revealed that others, studying a broad array of lizards, had made similar observations.

These observations were surprising because if any trait should be the subject of the daily scrutiny of natural selection Darwin envisioned, lizard legs would be near the top of the list. Ever since Arnold (1983) conceived of the morphology-performance-fitness approach to the study of natural selection, studies of lizard limbs have represented leading examples of how natural selection and evolutionary adaptation can be studied (Garland and Losos 1994; Le Galliard et al. 2004; Miles 2004; Olberding et al. 2016; Foster et al. 2018; Cordero et al. 2021; Norris et al. 2021; Zimin et al. 2024).

Specifically, studies at the macroevolutionary level have demonstrated the adaptive significance of limb length variation. Related species differing in limb length show evidence of adaptation to using different parts of the environment: limb length is correlated with differences in habitat use, behavior, and functional capabilities in many different clades (Losos 1990a, 1990b; Vanhooydonck et al. 2000; Bickel and Losos 2002; Herrel et al. 2002; Goodman et al. 2008; Foster et al. 2018). For example, in *Anolis* lizards, long-legged species use broad surfaces, are faster runners and longer jumpers, and use these capabilities to capture prey and elude predators. Conversely, shorter-limbed species are more dexterous, displaying enhanced ability to negotiate narrow and irregular surfaces, such as thin twigs (Losos 2009). Comparable patterns have been documented for many other lizard clades, such as chameleons (Da Silva and Tolley 2013) and Neotropical ground lizards (tropidurines; Kohlsdorf and Navas 2012).

Similarly, at the microevolutionary level, selection on limb length has been documented in field studies of many lizard species (Olsson et al. 2002; Losos et al. 2004; Husak et al. 2006; Calsbeek and Irschick 2007; Calsbeek et al. 2009; Donihue et al. 2018; Stroud et al. 2024). The explanation for the relationship between limb length and fitness has been enlightened by performance studies that have documented that variation in sprint speed among individuals is related to differences in limb length: longer-legged lizards, even with the effect of body size statistically removed, run faster (Losos and Sinervo 1989; Bauwens et al. 1995; Irschick and Losos 1998; Lowie et al. 2019). Sprint speed, especially for terrestrial species, is an important performance trait associated with many behaviors that have fitness consequences, such as predator avoidance and foraging ability (Irschick and Losos 1998; Miles 2004; Husak 2006a, 2006b).

These observations emphasize the apparent paradox at the heart of this article: if subtle differences in limb length

between individuals can affect performance, survival, and reproduction, how can a lizard missing a substantial portion—or even the entirety—of a limb not only survive but even thrive?

To explore this topic, we canvassed colleagues and posted social media inquiries to identify additional observations and data on lizard limb loss. While not intended to be a comprehensive review of limb loss, this article is the result of those efforts. We report that lizards with substantial limb loss have been observed throughout the Squamata (excluding limbless taxa). Population studies indicate that although such lizards occur at low levels within populations, at least some of these lizards not only survive but thrive despite missing some or all of a limb. In the discussion section, we consider whether the widespread but low-frequency occurrence of such individuals represents random noise or highlights an important perspective on how natural selection operates.

Methods

Review of Observations

To be included in our compilation, a lizard must have lost at least an entire foot and the injury must appear to be completely healed, indicating that the animal survived whatever caused the loss of limb. Most examples are documented with photographs, although some are based solely on data in field notes. Most records are from field studies, but some museum specimen observations are also reported. Additionally, some reports of species not included in our personal observations were gathered from published literature (17 of 122 records [table S1; tables S1, S2 are available online], most from a recent compilation of examples from Neotropical lizards; Cavalcante and Passos 2024). In several cases we also include population studies that provide information on the performance and fitness of limb-impaired lizards compared with limb-intact conspecifics.

At the outset, a caveat must be acknowledged: the observations reported herein are anecdotes collected in a haphazard way. No doubt, the observations are biased in many respects. A superficial interpretation of the data we present below might suggest that limb loss is often fairly innocuous to lizards. However, this interpretation overlooks an inherent survival bias in our dataset: lizards negatively affected by limb loss may die unnoticed, precluding their presence in our records.

Results

We found 122 records of limb loss from 58 species spanning the phylogenetic breadth of lizards, including 21 of 36 limbed lizard families (i.e., excluding amphisbaenids, dibamids, and snakes). Limb loss ranged from a forefoot to an entire limb (table S1). Caribbean lizards, particularly

in the genus *Anolis* (hereafter, “anoles”), constitute a disproportionate fraction of the dataset. We suspect that this imbalance does not reflect a greater occurrence of limb loss—or propensity to survive it—in anoles but rather is a function of the extent to which these lizards have been studied, as well as the research network of the authors.

Figure 1 provides photographs of several cases, and many others are presented in the supplemental PDF. Examination of these photographs indicates that many of the lizards seem to be healthy; very clearly, they are not emaciated but rather appear to be in good condition. In other words, the animals not only have survived the limb loss but do not appear to be experiencing decreased foraging success (i.e., they do not appear to be starving).

Types of Limb Damage

Limb injuries were classified by extent of loss (see table S1). Locomotion in most lizards, especially maximal sprint speed, is largely powered by the hindlimbs (Alexander 2003), and as such hindlimbs are typically substantially longer than forelimbs (Irschick and Jayne 1999). The difference in force generation is exemplified by the observation that many terrestrial lizards may temporarily transition to hindlimb bipedalism during maximal effort (Kinsey and McBrayer 2018). Consequently, it might be expected that missing forelimbs would be more prevalent in our dataset, on the assumption that animals losing part or an entire hindlimb would be less likely to survive than those with damaged forelimbs. The examples listed in table S1 do not support this prediction: slightly more than half of the reported cases of limb loss involve the hindlimb (65 of 122 examples; 53%). However, if we restrict our comparison to only the most severe injuries—when an entire limb is lost—our supposition is supported: only 5% of observations involved the loss of an entire hindlimb ($n = 6$), the rarest form of single-limb damage present in our dataset. In contrast, a dozen lizards were observed with full forelimb loss ($n = 12$); some of these individuals even had substantial damage to the other forelimb as well (table S1, e.g., ID 16; fig. 2C), whereas none of the individuals that had lost an entire hindlimb also had damage to the other hindlimb. It is therefore likely that the fitness consequences of limb damage are strongly governed by the type of limb damage incurred, with full hindlimb damage appearing to be the costliest (of course, an alternative possibility is that instead of resulting from different survival rates, our observations reflect the frequency with which different types of damage are incurred—perhaps full forelimb loss occurs twice as often as full hindlimb loss).

Similarly, one might expect loss of a hand or foot to be observed more than loss of an entire limb (for the sake of clarity, we will refer to forefeet as “hands” and to hindfeet as “feet” in this article). In this case, the data support the

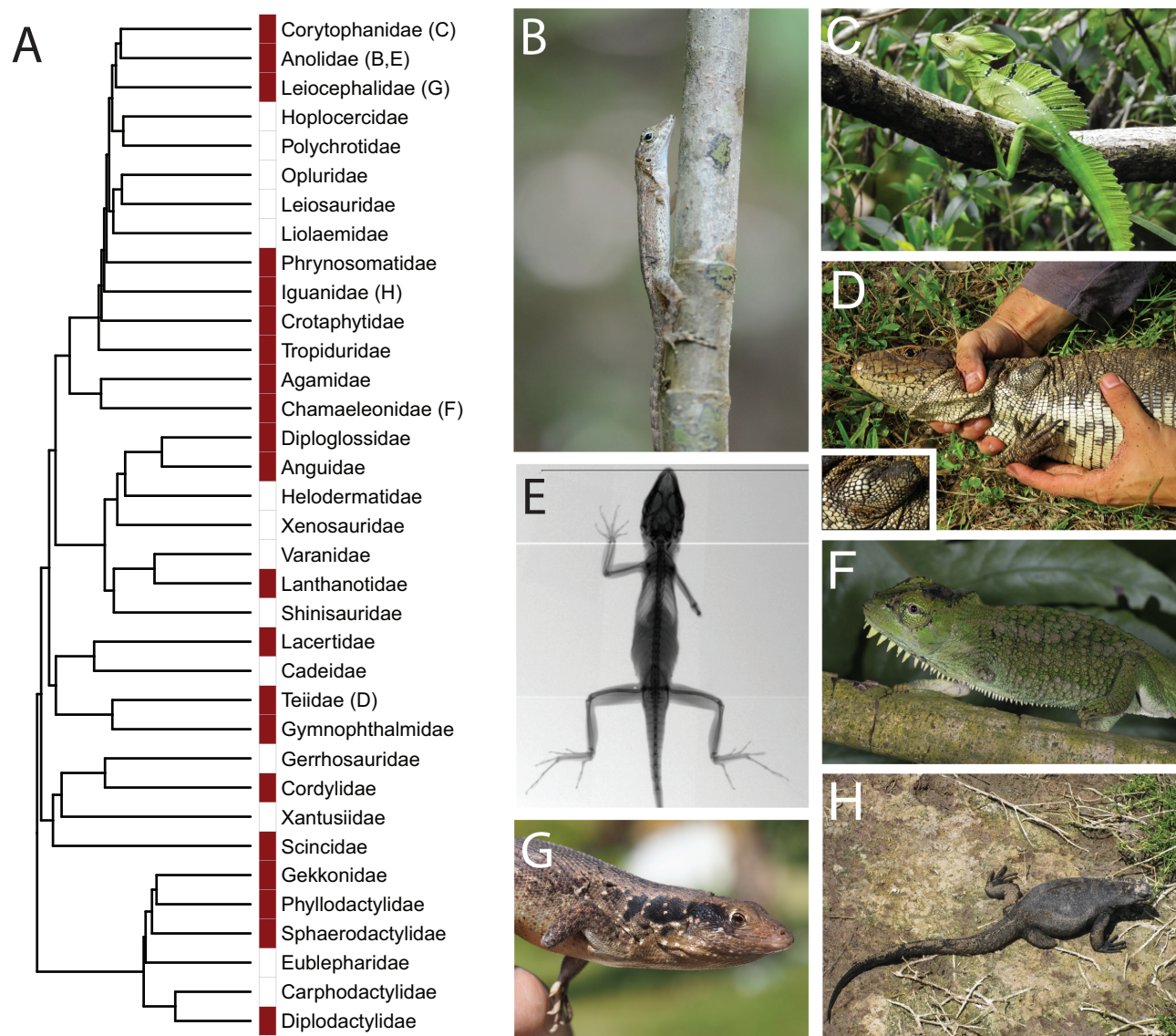


Figure 1: A, Records of limb loss are spread across a wide range of quadrupedal lizard families that employ a variety of different locomotor and ecological strategies. Filled squares represent families with records of limb loss in our dataset; unfilled squares are families with no records. Letters next to families correspond to species pictured opposite. Families composed entirely of limbless species are not included in the phylogeny. B, Puerto Rican crested anole (*Anolis cristatellus* [Anolidae], table S1, ID 7; M. Leal). C, Plumed basilisk (*Basiliscus plumifrons* [Corytophanidae], ID 60; J. Mora). D, Caiman lizard (*Dracaena paraguayensis* [Teiidae], ID 119; D. Passos; inset included for additional detail). E, Radiograph of a brown anole (*Anolis sagrei* [Anolidae], ID 29; J. Kolbe). F, Four-horned chameleon (*Trioceros quadricornis* [Chamaeleonidae], ID 54; C. Anderson). G, Rum Cay curlytail lizard (*Leiocephalus loxogrammus* [Leiocephalidae], ID 90; A. Geneva/N. Herrmann). H, Galapagos marine iguana (*Amblyrhynchus cristatus* [Iguanidae], ID 76; S. French). C was modified from Mora et al. (2020), licensed under CC BY-SA 4.0.

prediction only for hindlimbs. Slightly more lizards had lost a hand ($n = 16$) than an entire forelimb ($n = 12$), but we recorded 17 instances of hindfoot loss compared with just six lizards missing entire hindlimbs. The most common forms of limb damage were losing a hand ($n = 16$), a foot ($n = 17$), or a hindlimb up to the knee ($n = 16$).

Damage to two or more limbs was rarer (fig. 2); five lizards had lost part or all of both forelimbs (e.g., fig. 2C; table S1, IDs 16, 49, 64, 75, 82). No lizards were observed with damage to both hindlimbs. In instances where lizards suffered loss of both a forelimb and a hindlimb element, affected limbs were always contralateral (e.g., fig. 2A, 2B; table S1, IDs 20, 61). In other words, no lizards were observed with



Figure 2: Examples of damage to more than one limb. A, Brown basilisk (*Basiliscus vittatus* [Corytophanidae], table S1, ID 61) missing almost all of its forelimb and partially missing contralateral hindlimb (B. Hillen). B, Jamaican opal-bellied anole (*Anolis opalinus* [Anolidae], ID 20) missing most of a forelimb and lower contralateral hindlimb (D. Calder/L. Johnson/I. Maayan). C, Jamaican stripe-footed anole (*Anolis lineatopus* [Anolidae], ID 16) missing both forelimbs (A. Walker).

damage to both limbs from the same side of the body. Also, no lizards were observed with damage to three or all four limbs.

Cause of Limb Loss

We assume that most limb loss observations in our dataset are the result of trauma due to environmental factors, but we have only one direct observation of a limb loss event, which occurred when an *Anolis sagrei*'s leg was caught just below the knee in the lid of a trash can; the lizard ran away when freed, but the leg withered away at the point where it was pinned and subsequently fell off (fig. 3C; see the supplemental PDF for details of this event). Most likely limb loss usually is the result of failed predation attempts or agonistic interactions with other competitors, as in amphibians (Ballengee and Sessions 2009). Scars to the body of many

lizards with limb loss perhaps provide further evidence of the traumatic events that led to their limb damage (see figures in the supplemental PDF).

Occasionally, lizards are born with limb deformities (e.g., fig. S62), although this seems rare. For example, in a laboratory colony of brown anoles (*A. sagrei*), only two of 1,127 lizards hatched with limb deformities (0.2% of all hatchlings; J. M. Hall, unpublished data). The limb deformities in these two lizards likely resulted from a heat stress treatment (Hall and Warner 2019). More extreme developmental abnormalities of limbs can also exist; a Cuban knight anole (*Anolis equestris*) hatched with a partial hindfoot—containing three fully formed digits—attached to its right knee (fig. 1 in Muell and Gross 2023). While some of our limb loss records (table S1) could have resulted from such developmental abnormalities, direct observation of hatching in the wild is rare, making this possibility difficult to assess.

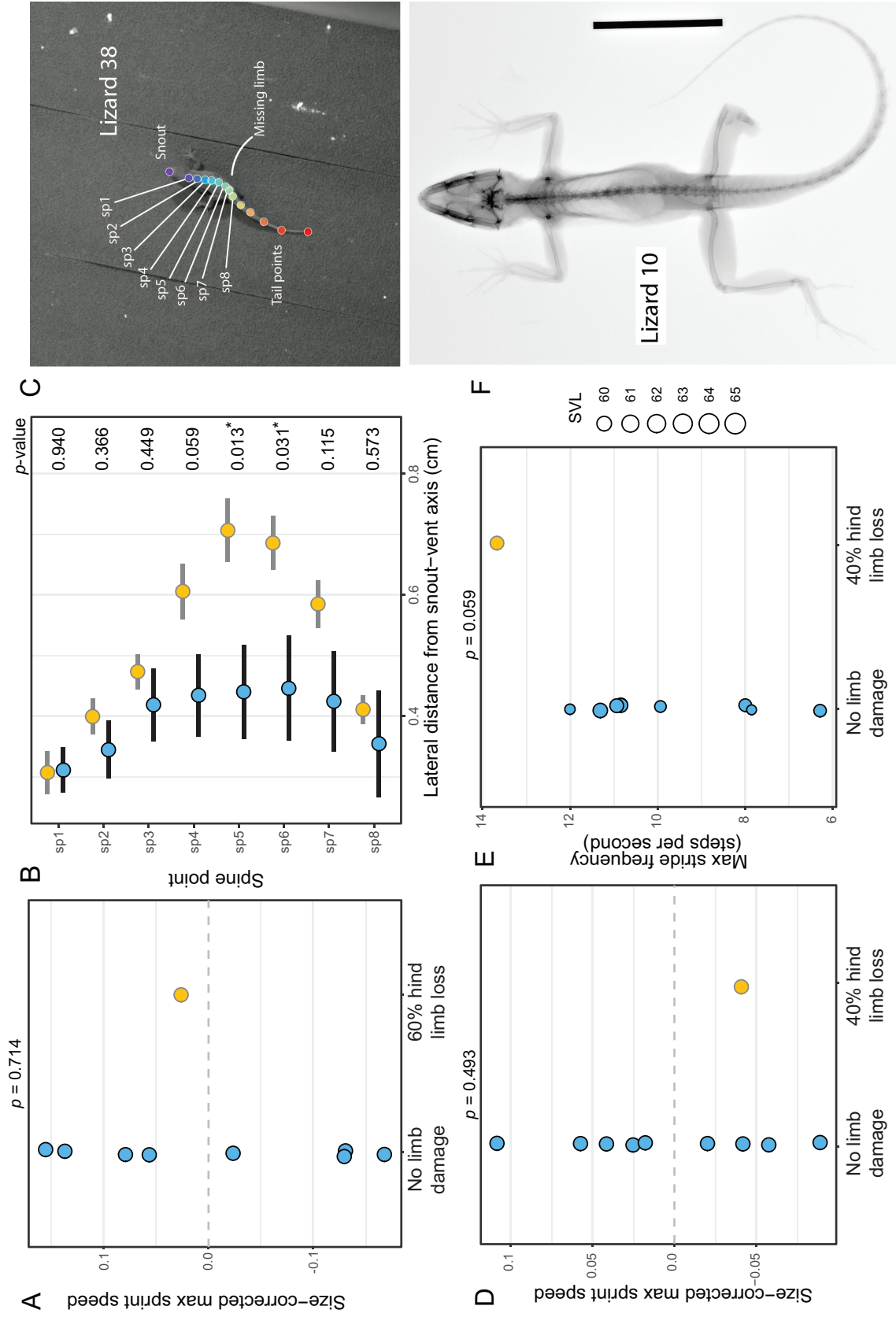


Figure 3: Comparative sprinting performance and kinematic analyses of limb-damaged *Anolis* lizards. A–C, Lizard 38, male Cuban brown anole (*Anolis sagrei*). Despite missing more than half of its right hindlimb, lizard 38 had comparable maximal sprinting performance with other male *A. sagrei* in the population (A). A major kinematic difference during sprinting was that lizard 38 displayed significantly greater trunk undulation (B), particularly in the midspine points, as annotated in C. Gray points represent lizard 38; black points represent data from seven comparably sized and fully limbed *A. sagrei*. Points represent mean values per frame; error bars represent 1 SE. D–E, Lizard 10, male Puerto Rican crested anole (*Anolis cristatellus*). Lizard 10 also had comparable sprint speed with other male *A. cristatellus* in the population (D), although it exhibited a faster stride frequency rate (E). In E, point size reflects body size (snout-vent length [SVL]). F displays a radiograph of lizard 10 showing back right hindlimb damage. Points are slightly jittered horizontally for visualization purposes (A, D, E). Photo credits: C. Anderson (C), J. Suh (F).

Limb Loss Frequency in a Population

Most examples collated in this study were opportunistic and collected haphazardly; therefore, it is difficult to determine how prevalent limb loss is in the population. However, in several cases the observations were from populations under study, so we can compute the proportion of lizards with damaged/healed limbs. Overall, lizards with limb element loss appear rare within populations (see table S2). Across 33 populations of nine species from seven families on four continents (North America, Australia, Africa, and Europe), the average proportion of limb-deficient lizards was 1.3% (when weighted for unequal number of sampled populations among species). With the exception of European common lizards (*Zootoca vivipara*), which had unusually high proportions of limb loss (table S2), all populations except one contained <1% of lizards with limb loss (the exception was a small population of *Sceloporus grammicus*; 1 of 31 lizards = 3.23%; all other population sizes ranged from 153 to 1,212 lizards; table S2). Of course, the true proportion of lizards with limb loss in natural populations is likely lower, as these datasets were recruited from researchers who reported limb loss to us—study populations with no lizards with limb loss did not come to our attention.

Limb Regeneration Capabilities

Unlike the ability of some lizards to regenerate tails lost through autotomy, lost limbs cannot be fully regenerated. However, limited ability to regenerate limb structures has been demonstrated in some lizards (Alibardi 2022). In general, these regenerated limbs are composed of cartilage rather than bone (for a review, see Alibardi 2022), as has been documented in several species (Bellairs and Bryant 1985; Pasachnik 2011; Carbajal-Márquez and Valdez-Villavicencio 2012; Cavalcante and Passos 2024). While such cartilaginous structures presumably do not fully restore locomotor performance, the regenerated tail-like limbs apparently help the lizard to “move rapidly in their environment” (Alibardi 2022). Video S5 (videos S1–S5 are available online) illustrates such rapid movements by an *A. sagrei* with a cartilaginous regenerated limb (fig. S25 is a corresponding radiograph).

Performance Costs

To our knowledge, no study has explicitly tested the effect of limb loss on locomotor capabilities in lizards (although the biomechanics of lizards that have evolutionarily lost limbs, including snakes, has attracted substantial research attention; Gans 1986; Russell and Bels 2001; Camaiti et al. 2021; Chong 2022a, 2022b). Nonetheless, given that even slight differences in limb length lead to detectable differences in sprint speed (Bonine and Garland 1999; Zamora-Camacho

et al. 2014; Lowie et al. 2019) and, interspecifically, jump distance (Losos 1990a), it is typically assumed that losing part or all of a limb must have negative consequences on locomotor performance.

Sprint Speed. Sprint speed data were collected for limb-deficient lizards along with data for fully limbed lizards from the same populations in four studies (see the supplemental PDF for methods and other details on performance studies). The results did not indicate an exceptional impact of limb loss on sprint speed. In the first study, an eastern fence lizard (*Sceloporus undulatus*) missing the foot and tibia of its right hindlimb had slightly faster sprint speed than expected for its body size (sprint speed generally correlates with body size in lizards; Garland and Losos 1994; fig. S63). In the second study examining a French population of *Z. vivipara*, three females with limb loss were inspected: one with forelimb loss and another with hindlimb loss both ran as fast as expected for their body size relative to other females, while another with forelimb loss ran faster than expected (fig. S64; no data are available on the extent of limb loss for these lizards). In the third study, an *Anolis cristatellus* from its introduced range in Miami, Florida (Stroud et al. 2020), missing its foot and lower portion of the tibia (lizard 10; fig. 3F) ran slower than expected for its body size but still ran faster on a size-corrected basis than some fully limbed lizards. Video analysis of this *A. cristatellus* revealed that the injured lizard exhibited substantially faster stride frequency than uninjured lizards (fig. 3E; see the supplemental PDF). In the fourth study, we investigated the sprinting kinematics of an *A. sagrei* (lizard 38; table S1, ID 38), which had lost more than half of its right hindlimb yet ran faster than expected for its body size (fig. 3A; see the supplemental PDF). Using a deep learning video analysis tool (DeepLabCut; Mathis et al. 2018), we observed that lizard 38 exhibited substantially exaggerated trunk undulation (fig. 3B; Pillai's trace = 0.795, $F_{1,23} = 7.73$, $P < .001$). Specifically, undulation was most exaggerated in the mid-body, especially at spinal points 4 ($F_{1,23} = 3.94$, $P = .059$), 5 ($F_{1,23} = 7.31$, $P = .013$), and 6 ($F_{1,23} = 5.30$, $P = .031$; fig. 3B, 3C). In tetrapods that exhibit sprawled posture, such as lizards, locomotor propulsion can be aided by increasing the rate of lateral body undulation (Farley and Ko 1997), suggesting that this was a compensatory strategy for maintaining comparable sprint speed.

In summary, two lizards with limb deficiencies ran more quickly than conspecifics with intact limbs on a size-corrected basis, two exhibited no effect of limb loss on sprint speed, and only one exhibited a decrement in sprint speed. Given the strongly established relationship between limb length and sprint speed in lizards, this result is unexpected. Biomechanical analysis gives a hint at the explanation—both of the limb-damaged lizards for which we have biomechanical

data altered their stride mechanics to compensate for their shorter limbs.

Endurance. We tested for differences in endurance between lizards with and without limb injuries from 21 populations of *Z. vivipara* (D. B. Miles, J. Clobert, and M. Massot, unpublished data). Overall, lizards with limb loss had similar endurance to those without limb loss (fig. S64) in both males (average injured endurance = 295 ± 156 [1 SD] s [$n = 13$] vs. uninjured = 299 ± 189 s [$n = 132$]) and females (average injured endurance = 138 ± 42 s [$n = 16$] vs. uninjured = 150 ± 55 s [$n = 281$]).

Jumping. We also measured the maximal jumping performance of lizard 10 (missing 40% of its right hindlimb; fig. 3F) versus similar-sized male *A. cristatellus* ($n = 10$). When encouraged to jump from a 10-cm-wide horizontal branch positioned 50 cm from the ground, lizard 10 had a maximum jump of 43 cm. Other males ranged from 54 to 90 cm. When accounting for body size, lizard 10 had a significantly shorter jump capability than limb-intact lizards ($F_{1,8} = 5.86$, $P = .042$).

Body Condition Comparisons

We might expect that lizards with limb loss would be less proficient at foraging and thus would exhibit poorer body condition (i.e., weigh less for their body size relative to other lizards in the population). However, that does not appear to always be the case. We had data on the body condition (i.e., the relative weight of a lizard compared with others in its population) of 21 limb-deficient lizards (table 1). Nine injured lizards were heavier than expected for their body size, whereas 12 injured lizards were lighter than expected for their body size; the probability of observing 12 or more lizards out of 21 being lighter than expected, assuming equal chances of being heavier or lighter, is approximately 49%.

Although foraging costs might be expected to be greatest with substantial versus minimal limb loss, the degree of limb loss did not seem to correlate with body condition. For example, of the three injured lizards more than 40% heavier than expected for their body size, two side-blotched lizards (*U. stansburiana*) had lost just a hand but an elegant snake-eyed skink (*Cryptoblepharus pulcher*) was missing an entire hindlimb (table 1). Conversely, the “lightest” injured lizard was a brown anole (*A. sagrei*) missing half of a hindlimb that was 20% lighter than expected for its body size. Overall, whether the injury was to a forelimb or a hindlimb did not appear to influence body condition: four of nine lizards with forelimb injuries (44%) and five of 12 lizards with hindlimb injuries (42%) were heavier than expected for their body size. In sum, although few data ex-

ist, it does not appear that limb-damaged lizards consistently show evidence of major costs to body condition (table 1).

Reproductive Status

Little information is available about the influence of limb loss on reproduction. Two male lizards with limb loss were observed mating (*A. sagrei* [J. B. Losos, personal observation], *Crotaphytus collaris* [A. R. Templeton, personal observation]), and some females contained oviductal eggs, suggesting that mating had occurred (*Glaucomastix littoralis* [D. C. Passos, personal observation], *A. sagrei* [G. Norval, personal observation], *U. stansburiana* [P. A. Zani, personal observation]). An adult female Puerto Rican crested anole (*A. cristatellus*; table S1, ID 11; fig. S9) caught in Miami missing its entire right hind foot had above average fat mass deposits (0.067 vs. uninjured average = 0.033 g) and body condition (table 1, ID 11) and was classified in the most advanced reproductive stage of female anoles, possessing one yolky ovarian follicle and two oviductal eggs (i.e., reproductive stage 4; Sexton et al. 1971; Hall et al. 2020, 2024). In sum, she appeared to be in healthy reproductive status.

Long-Term Survival

Records of three-legged lizards in survival studies are also scarce, but some data exist. In several cases, limb-deficient lizards survived for a long time. In Tennessee, an individual *Anolis carolinensis* missing its lower forelimb was the longest-lived animal in a monitored population (*A. C. Echternacht*, personal observation; table S1, ID 5). In Australia, a velvet gecko (*Oedura lesueurii*) survived at least 6 months after initial capture when limb damage was first observed (D. A. Pike, personal observation; table S1, ID 69). In Missouri, a yearling eastern male collared lizard (*C. collaris*) captured in July 1999 with a missing forelimb (fig. S40) lived more than 4 years, substantially longer than the expected lifespan for males in that population (1.75 years at birth, 2.75 years for yearlings; A. R. Templeton, unpublished data).

On the other hand, survival of other limb-deficient lizards was low. In tagged populations of common side-blotched lizards (*U. stansburiana*) in Oregon (table S1, IDs 101–105) and Nevada (table S1, IDs 99, 100), limb-damaged lizards ($n = 7$) were never observed again after initial recording, suggesting that they did not survive (P. A. Zani, personal observation). Similarly, in Florida two three-legged adult brown anoles (*A. sagrei*; figs. S32, S33) appeared to be in healthy body condition (table 1, IDs 43, 44), but neither survived to the next sampling period 6 months later. It must be noted, however, that most lizards in these two studies did not survive

Table 1: Body condition of injured lizards relative to uninjured lizards

Injured limb, table S1 ID	Limb damage (%)	Species	Location	Sex	N	Body condition (residual)	Lighter/ heavier (%)	Body condition percentile
Forelimb:								
106	20	<i>Uta stansburiana</i>	Utah (USA)	Male	NA	.679	+97.2	NA
107	20	<i>Uta stansburiana</i>	Utah (USA)	Female	NA	.367	+44.3	NA
29	40	<i>Anolis sagrei</i>	Bahamas	Female	17	-.133	-12.5	17.6
22	40	<i>Anolis sagrei</i>	Bahamas	Female	8	.042	+4.3	62.5
30	40	<i>Anolis sagrei</i>	Bahamas	Male	15	-.065	-6.3	26.7
23	40	<i>Anolis sagrei</i>	Bahamas	Male	12	-.014	-1.4	50.0
31	60	<i>Anolis sagrei</i>	Bahamas	Female	6	-.152	-14.1	16.7
43	80	<i>Anolis sagrei</i>	Florida (USA)	Female	363	.077	+8.0	82.6
6	100	<i>Anolis carolinensis</i>	Alabama (USA)	Male	17	-.002	-.2	52.9
Hindlimb:								
11	20	<i>Anolis cristatellus</i>	Florida (USA)	Female	13	.017	+1.7	69.2
69	20	<i>Oedura lesueurii</i>	Australia	Juvenile	173	-.197	-17.9	21.4
98	20	<i>Urosaurus ornatus</i>	Arizona (USA)	Female	NA	-.182	-16.7	NA
25	40	<i>Anolis sagrei</i>	Bahamas	Female	6	-.228	-20.4	16.7
9	40	<i>Anolis cristatellus</i>	Florida (USA)	Male	319	-.123	-11.6	10.7
94	60	<i>Sceloporus undulatus</i>	Alabama (USA)	Male	18	.039	+4.0	83.3
22	60	<i>Anolis sagrei</i>	Bahamas	Female	15	-.031	-3.1	40.0
41	60	<i>Anolis sagrei</i>	Florida (USA)	Male	224	-.001	-.1	48.7
76	60	<i>Amblyrhynchus cristatus</i>	Ecuador	Female	NA	.080	+9.0	NA
26	80	<i>Anolis sagrei</i>	Bahamas	Male	13	-.021	-2.1	53.8
108	100	<i>Uta stansburiana</i>	Utah (USA)	Male	NA	.160	+17.3	NA
111	100	<i>Cryptoblepharus pulcher</i>	Australia	Juvenile	38	.340	+40.5	73.7

Note: Each row represents a single injured lizard (for reference, see the ID column of table S1) whose body condition was compared with that of conspecifics in the same population. In cases in which the sex of lizards was recorded, injured lizards were compared only with uninjured conspecifics of the same sex (N). Body condition was calculated as the residual from an ordinary least squares regression of log-transformed body length against log-transformed mass. The $\pm\%$ values show how much heavier or lighter each injured lizard was compared with what we would expect for a lizard of that length in that population. Body condition percentiles indicate the percentage of the population that has a body condition equal to or less than that of the injured lizard. NA = data not available.

to the next sampling period regardless of limb condition (see the supplemental PDF for more information).

Discussion

Variation in limb length among lizards is a paradigmatic example of evolutionary adaptation. Given the established adaptive significance of limb length, reasonable hypotheses about the effect of limb loss might include that it reduces the survival, health, and welfare of lizards, perhaps by reducing their locomotor performance. Taken at face value, the case studies that we have assembled indicate that the consequences of limb loss may sometimes be less severe than hypothesized, even for lizards that lose an entire limb. For example, many of the lizards in our dataset do not appear

to have incurred a high foraging cost, appearing healthy and well nourished (figs. 1, 2). In cases where quantitative data were available, the body condition of limb-deficient lizards, corrected for body size, was often comparable or superior to that of uninjured lizards (table 1), and some limb-impaired lizards were reproductively active. Longitudinal data, when available, revealed mixed results. Some limb-deficient lizards survived longer than most fully limbed individuals, while others were not observed to survive spans of 6 months or less between sampling periods (although low survival of all lizards in these populations means that limb damage may not be the cause of the quick demise of limb-deficient lizards).

The performance consequences of limb loss or damage are also surprisingly ambiguous. In many lizards, it is well

established (both inter- and intraspecifically) that limb length correlates with sprint speed, primarily because longer legs allow for longer strides (Bauwens et al. 1995; Bonine and Garland 1999). Consequently, we would expect lizards missing part or all of a limb to exhibit substantially reduced sprint speed due to decreased stride length and asymmetries between the right and left limbs. Remarkably, the limited quantitative data available show no such effect (fig. 3). Qualitatively, many lizards with limb loss seemed to move normally (see the supplemental videos), to the extent that some lizards were not noticed to have limb injuries until captured. Biomechanical analysis of two *Anolis* lizards with injuries (lizards 10 and 38; fig. 3) revealed apparent compensatory mechanisms that allowed for comparable maximal sprint speed to fully limbed lizards: lizards with limb loss had a faster stride rate (fig. 3E) and substantially greater lateral flexion of the midbody (fig. 3B; see the supplemental PDF for discussion of why the two lizards may have compensated in different ways and other possible ramifications of altering stride dynamics).

Of course, the types of short-term laboratory performance (sprinting and jumping) assays presented in our study may or may not accurately reflect long-term performance in the wild (e.g., survival, foraging, or reproductive success). For example, despite compensatory mechanisms appearing to be effective strategies, could there be hidden long-term fitness costs? One possibility is that the biomechanical shifts we observed, such as increased flexion and rate of strides, could be more energetically expensive than typical locomotion. If so, it is possible that by altering their gaits, both injured lizards maintained comparable sprinting speed but at the cost of greater energetic expenditure, which could ultimately incur future fitness costs. In any case, endurance data—available only from French common lizards (*Zootoca vivipara*) in our dataset—did not reveal any differences in stamina (i.e., time taken to reach fatigue when running) between lizards with or without limb injuries.

Clearly, more data on the performance consequences of limb loss would be useful, and we encourage researchers to seize the opportunity to collect such data when limb-deficient lizards are discovered. An interesting question is whether lizards vary in their ability to compensate biomechanically for limb injuries—it could well be the case that those that can compensate survive, whereas those that can't do not. One innovative approach to exploring this would be with lizard-inspired quadrupedal robots (Chong et al. 2021, 2022a, 2022b, 2023), which open new possibilities for experimental studies of how limb loss affects locomotor biomechanics.

Despite the evidence that many lizards survive dramatic injuries, some showing no reduction in their functional capabilities, we reiterate why our data compilation cannot be taken at face value: lizards suffering the detrimental consequences of

limb loss may perish quickly, their existence never detected by biologists. Undoubtedly, selection pressures against limb loss are probably very high. Still, is it not remarkable that some lizards are able to survive despite such handicaps? Many would be amazed that our compilation includes 18 lizards missing an entire limb, some observed moving with such agility that they were hard to capture. Or consider the remarkable locomotor adaptations of chameleons, whose digits are fused into two opposing pads that can zygodactylously¹ grasp even the narrowest of branches and that moves by swaying back and forth like a leaf in the wind, slowly moving contralateral limbs forward while the other two limbs continue grasping the branch. How can such an animal survive without one of its arms? We propose four possibilities.

Possibility 1: Natural Selection Is Probabilistic

Natural selection occurs when phenotypic differences are associated with differences in mean fitness. However, individuals with the same phenotype can vary in fitness due to life's contingencies. To view through an organismal lens: if a three-legged lizard never encountered a predator, then reduced sprint speed—if it was incurred—may not have been detrimental to survival. In other words, while natural selection favors traits that improve an organism's average fitness, the actual fitness of an individual organism is influenced by various factors and events in its life, making the process of natural selection probabilistic rather than deterministic.

Possibility 2: Natural Selection Is Multifarious

Selection operates on multiple traits simultaneously. It is possible that some three-legged lizards possess other “high-quality” traits whose benefits offset the detriment caused by limb impairment. For example, a lizard with exceptional eyesight may not need to run quickly to evade predators, minimizing the survival costs of limb loss relative to other lizards that suffer the same fate. This possibility might explain why so many limb-impaired lizards appear to be in good physical condition; rather than indicating that selection is not operating on limb length, the existence of limb-impaired lizards in good physical condition might indicate that only lizards that were in excellent condition beforehand might be capable of surviving such an injury.

1. The term “zygodactylus” was first used to describe bird foot structure (Coues 1890, p. 187) and has also been used historically to describe chameleon foot structure. However, this usage does not accurately reflect the digit-grouping pattern of chameleons, which differ from zygodactylus birds in having five versus four digits, respectively. A new and more precise term, “chamaeleodactylus,” has been suggested to better describe the unique digit arrangement in chameleons and would appear more appropriate.

Hendry et al. (2022) have presented the converse perspective to ours. Instead of focusing on how the possession of superior traits may allow the survival of individuals with other, suboptimal traits, they pointed out how the occurrence of limb injuries and associated negative costs could disrupt or weaken prevailing patterns of selection if they occur in individuals that would otherwise possess high fitness. As such, if there are fitness costs associated with limb loss or injuries, then such events could represent a source of randomness in evolution, ultimately limiting the power and precision of local selection pressures (Hendry et al. 2022). These contrasting views on how superior and inferior traits in the same individual may affect fitness are not contradictory; both may hold true in different situations.

Possibility 3: Natural Selection Is Episodic

Selection on a trait may vary through time. Recent discussions have challenged the Darwinian view of omnipresent selection, instead arguing that natural selection occurs in discrete, intermittent events (Vermeij 2023). Instead of being all encompassing, natural selection may represent a fluid force that varies through space and time (Stroud et al. 2023). Sometimes sprint speed or endurance is crucial, other times—perhaps when prey are superabundant or predator populations are low—it may not matter at all. Perhaps the three-legged lizard examples in our collation (table S1) come from populations experiencing a period of weak or relaxed selection on limb length; had researchers sampled at a different time—for example, when food was scarce or the abundance of conspecifics or predators high—they might have encountered no such individuals. In effect, the limb-damaged lizards that we observed may have been lucky to be alive at the right time given their condition. At present, we have an incomplete understanding of the long-term dynamics of natural selection in the wild because of the paucity of studies that measure the consistency of selection pressures through time (Stroud and Ratcliff 2025).

Possibility 4: Behavior Is the Filter between Organism and the Environment

The morphology-performance-fitness paradigm assumes that the morphology of a given organism reflects a consistent performance ability that translates to a constant fitness value (Arnold 1983, p. 198): if an organism possesses a morphology that produces suboptimal performance relative to other members of the population, then it will experience lower fitness. An alternative possibility, however, is that an organism may instead simply change its behavior to avoid situations that necessitate performance activities for which they are suboptimal, avoiding the predicted fitness costs (Garland and Losos 1994). For example, lizards with low sprint speed ca-

pabilities due to limb loss may switch habitats or adopt behaviors—for example, more stalking and greater reliance on crypsis—that do not require rapid movements. Similarly, such lizards may instead spend more time near a refuge, such as a rock crevice or a burrow in saxicolous species, which requires only a short dash to safety. In this sense, behavior may serve as a buffer or “shield” that limits exposure to agents of selection that might otherwise affect the organism (Bogert 1949; Huey et al. 2003; Muñoz 2022).

More generally, these observations highlight the need for greater examination of how individual behavior integrates into the morphology-performance-fitness relationship (Garland and Losos 1994). Field studies that attempt to measure fitness directly on variation in performance or behavior remain rare compared with morphology-fitness approaches (but see Santos et al. 2015; Ballew et al. 2017; Lapiedra et al. 2018), but they would clearly be a valuable contribution to understanding how natural selection operates. This view is complementary to the appreciation that the environment does not impose selection on organisms but rather that organisms take an active role in defining how they interact with their environments and thus what selection pressures they experience (Lewontin 1970; Wake et al. 1983; Day et al. 2003). A clearer integration of this perspective into field studies of natural selection would also be worthwhile.

As well as changes in behavior, other forms of plasticity could also disrupt morphology-performance relationships. As we previously suggested, lizards capable of altering their locomotor dynamics may be able to compensate for limb injuries and maintain suitable performance abilities, while those unable to do so may not survive. A more extreme example is the famous Slijper's goat (Slijper 1942; West-Eberhard 2005), which not only managed to walk on its hind legs because of a congenital defect that rendered its front legs unusable but, concomitantly through ontogeny, developed many skeletal and muscular features that enhanced its ability to walk in this manner. One may question whether such a goat could survive in nature, but we do have in our dataset an anole from Jamaica that lacked both forelimbs (*Anolis lineatopus*; fig. 2C; table S1, ID 16) and was observed moving bipedally, “hopping around just using his back legs” (A. Walker, personal observation; fig. 2C). Unfortunately, nothing is known about that lizard's internal anatomy and whether it had developed similar features to Slijper's goat.

Are Lizards Special?

Could organismal responses to limb injuries themselves be under selection? If limb injuries occur consistently in the wild, selection could favor traits, either healing or compensatory, that minimize their impact. Our compilation suggests that lizards might be a suitable taxon to address this possibility. Not only is limb loss phylogenetically

widespread in lizards inhabiting myriad different environments (table S1), but lizards appear to demonstrate a range of compensatory mechanisms that facilitate locomotion and other movement behaviors (e.g., fig. 3). This possibility raises two questions. First, are lizards more prone to limb loss than other taxa? Although scarce, some published observations of limb loss, or serious limb damage, exist for other vertebrate groups (Arlet et al. 2009; Stephens et al. 2018; Detwiler et al. 2019; Hendry et al. 2022), suggesting that a broader comparative analysis would be useful. Second, if lizards are more prone to such injuries, have compensatory mechanisms evolved? For example, could lizards have evolved to heal more quickly from limb injuries? Lizards possess healing mechanisms in response to other injury types (e.g., tissue healing following tail autotomy; McLean and Vickaryous 2011), suggesting that it may be possible.

Conclusion: Macroevolutionary Implications

In our experience, most biologists have treated wild animals observed surviving major irreversible injuries as little more than a curiosity; certainly, consideration of the evolutionary significance of such incidents has been greatly neglected (but see Hendry et al. 2022). Some might dismiss the observations and data we have compiled as flukes, assuming that the vast majority of similarly injured lizards perished, and what we see is just the few lucky individuals that somehow survived. To the contrary, the existence of such lizards has highlighted to us several important unresolved questions about how natural selection operates. Three key points are worth emphasizing. First, more detailed studies exploring these perspectives in both lizards and other organisms would be valuable. Second, evolutionary biology would benefit from field studies that measure natural selection on multiple aspects of the phenotype, such as behavior and physiology, as well as morphology. And last but perhaps most importantly, these observations underscore a broader principle in evolutionary biology: the essential role of natural history. By documenting the unexpected, the trivial, or even the uninteresting, natural history observations not only can document important phenomena worthy of study but can also be the catalyst that sparks new conceptual perspectives (Greene 2005; Tewksbury et al. 2014).

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Statement of Authorship

J.T.S. and J.B.L. conceptualized the research. All authors contributed data. J.T.S., B.D., and T.L.C. curated and validated data. J.T.S. and B.D. completed statistical analyses. J.T.S. and J.B.L. wrote the first draft of the manuscript. All authors contributed to manuscript revisions.

Data and Code Availability

All raw data images, videos, and supplementary files are available on Figshare (<https://doi.org/10.6084/m9.figshare.28625105>; Stroud et al. 2025).

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