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The Bogert effect, a factor in evolution

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Behavior is one of the major architects of evolution: by behaviorally modifying how they interact with their environments, organisms can influence natural selection, amplifying it in some cases and dampening it in others. In one of the earliest issues of *Evolution*, Charles Bogert proposed that regulatory behaviors (namely thermoregulation) shield organisms from selection and limit physiological evolution. Here, I trace the history surrounding the origin of this concept (now known as the "Bogert effect" or "behavioral inertia"), and its implications for physiological and evolutionary research throughout the 20th century. A key follow-up study in the early 21st century galvanized renewed interest in Bogert's classic ideas, and established a focus on slowdowns in the rate of evolution in response to regulatory behaviors. I illustrate recent progress on the Bogert effect in evolutionary research, and discuss the ecological variables that predict whether and how strongly the phenomenon unfolds. Based on these discoveries, I provide hypotheses for the Bogert effect across several scales: patterns of trait evolution within and among groups of species, spatial effects on the phenomenon, and its importance for speciation. I also discuss the inherent link between behavioral inertia and behavioral drive through an empirical case study linking the phenomena. Modern comparative approaches can help put the macroevolutionary implications of behavioral buffering to the test: I describe progress to date, and areas ripe for future investigation. Despite many advances, bridging microevolutionary processes with macroevolutionary patterns remains a persistent gap in our understanding of the Bogert effect, leaving wide open many avenues for deeper exploration.

KEY WORDS: Behavioral drive, behavioral inertia, phylogenetics, physiology, rates of evolution.

Organisms are routinely faced with many abiotic and biotic pressures that impact their survivorship, growth, and reproductive success. For example, a lizard's ability to perform fitness-based tasks (like foraging or predator evasion) is limited by the thermal dependence of its performance, its hydric and metabolic economy, and its morphological dimensions (Angilletta 2009). Yet, organisms are not exclusively at the whim and mercy of their surroundings. Of key importance is the preeminent role that organisms exert on their own selective environments and, correspondingly, on their evolution (Mayr 1963; Brandon 1988; Odling-Smee 1988; Huey et al. 2003). Perspectives on the role of behavior in evolution generally fall into two nonmutually exclusive categories. Perhaps the more classic perspective is that behavior is a "motor" for evolution: through their behavior, organisms can exploit new resources in their environments or enter new habitats altogether, in turn exposing them to selection, driving evolution, and, potentially, promoting speciation (e.g., Mayr 1959, 1963; Wyles et al. 1983; West-Eberhard 1989; Gittleman et al. 1996; Blomberg et al. 2003; Sol et al. 2005).

By contrast, behavior can also serve as a "brake" on evolution. Central to this idea is the Bogert effect (or "behavioral inertia") (Huey et al. 2003), which describes the restraining role homeostatic behaviors (like thermoregulation or hydroregulation) exert on evolution. When confronted with novel conditions, organisms can preferentially select microhabitats to which they are already well adapted, thus maintaining homeostasis within their ancestral range. Doing so can reduce exposure to selection, in turn limiting evolution (Huey et al. 2003, 2012; Muñoz and Bodensteiner 2019). Although the concept of "behavioral inertia" was formalized in the early 21th century (Huey et al. 2003), the foundational ideas and observations behind it emerged more than half a century earlier in one of the earliest issues of *Evolution* (Bogert 1949).[1] In honor of the 75th anniversary of the

[1]The title of this article is a nod to Bogert's (1949) foundational study in *Evolution*, entitled "Thermoregulation, a factor in reptile evolution."

Society for the Study of Evolution, this piece celebrates and unpacks the cross-disciplinary importance of Bogert's foundational work, considers key progress to date, and proposes avenues for future exploration. I begin by describing the historical context surrounding Bogert's (1949, 1959) seminal studies, the conceptual and empirical progress that emerged in the following decades, and the modern formalization of the phenomenon (Huey et al. 2003). The foundational work (and the lion's share of follow-up research) has centered around thermoregulatory behavior, particularly in squamate reptiles (lizards and snakes), so that focus will be strong here, as well. Nonetheless, the principles discussed certainly apply to myriad homeostatic behaviors and lineages (Huey et al. 2003). As is true for many bold evolutionary ideas from the pre-phylogenetic era, some of the more provocative macroevolutionary implications of the Bogert effect have only been recently put to the test and, as will become evident, there is much we still do not know. Study of the Bogert effect is ripe for deeper evolutionary exploration (at both micro- and macroevolutionary scales, and across multiple types of homeostatic behaviors), and that this goal is increasingly within reach. I share progress to date and highlight promising avenues (and relevant methodological approaches) for future exploration. The concepts of "behavioral drive" and "behavioral inertia" have historically been studied independently, but I show how these concepts are interrelated and, in some cases, mutually dependent phenomena. Lastly, I consider some of the extended (but rarely tested) implications of the Bogert effect, for example, for macroevolutionary patterns of physiological diversity, niche conservatism, and speciation.

Setting the Stage: Early Work on Thermal Behavior

The mid-20th century—when seminal ideas about thermoregulation and physiological evolution were originally articulated—was a time of great intellectual upheaval in biology, dominated by a pull toward centralization and integration (Smocovitis 1992). By infusing evolution with genetic principles, the Modern Synthesis galvanized a new generation of evolutionary research (Huxley 1943). The fields of paleontology, taxonomy, and genetics were coalescing around a shared society (soon to be the Society for the Study of Evolution): one of the major goals of this nascent organization was to discover principles of micro- and macroevolution that could be gleaned by combining insights among previously isolated biological fields (Smocovitis 1994a,b). It was against this backdrop of unification zeitgeist that Raymond Cowles and Charles Bogert, two prominent North American herpetologists, made their seminal contributions integrating ecology, thermal physiology, and evolution (Cowles 1939, 1941; Cowles and Bogert 1944; Bogert 1949, 1959).

One of their foundational studies took place in Coachella Valley, California,[2] a region that hosts a wide diversity of Sonoran reptiles. In that study, Cowles and Bogert (1944) reported a number of key thermal traits for desert squamates (lizards and snakes), including heat tolerance, activity body temperatures, and voluntary thermal limits. Most remarkable among their results was a clear visualization of the stability in activity body temperatures among desert snakes and lizards. Activity temperatures, they found, did not simply correlate with the local thermal environment, and desert lizards were not exceptionally warm adapted (which had been a common viewpoint; e.g., Hesse et al. 1937). Rather, the most distinguishing thermal factor among species was diel activity, with diurnal species exhibiting higher activity temperatures than their nocturnal counterparts (a pattern that still holds true; e.g., Meiri et al. 2013; Moreira et al. 2021). This study by Cowles and Bogert (1944) established a clear role for thermoregulation as a key mitigating factor for reptile thermal relations, which disrupted long-standing dogma that reptiles were consummately "cold-blooded" and lacked the ability to regulate their core temperature (e.g., Agassiz and Gould 1856).

Although the observations made by Cowles and Bogert (1944) planted important seeds regarding the ameliorating role of behavior for reptile thermal biology, the inference space of their observations was limited by their study centering in a single locality. In a crucial follow-up study in *Evolution*, Bogert (1949) compared patterns of body temperatures between different species of whiptails (*Aspidoscelis*) and spiny lizards (*Sceloporus*) at field sites in Arizona and Florida. The climatic conditions varied substantially among the sites, setting up the possibility that thermal patterns might also differ (if a species' physiology reflects its local environment). Yet, Bogert (1949) was struck by the similarities in body temperature among localities, reflecting the "astonishing amount of control" (p. 202) the lizards exerted over their own temperature. He extended these observations even more broadly, and remarked that "closely related forms, even though they are sometimes placed in separate genera, tend to have thermal preferences, or normal activity ranges, that are extraordinarily close, despite marked dissimilarities in their habitats" (p. 202).

Bogert's (1949, 1959) observations were inherently evolutionary: his focus on stability in thermal relations among species, for example, implies at least some measure of evolutionary "stasis" or "rigidity" driven by behavioral homeostasis. Others echoed this general view of behavior as a key arbiter of environmental variation, and as an important stabilizing force in evolution (e.g., Bartholomew 1958, 1964; Hertz 1981; Wake et al.

[2]For readers familiar with the annual Coachella Valley Music and Arts Festival, the location is one and the same.

1983; Brandon 1988).[3] Bartholomew (1964) pushed this idea a bit further by implying some measure of phylogenetic inertia in trait evolution, stating that "all animals are caught in a phylogenetic trap by the nature of past evolutionary adjustments" (p. 11). Bogert's (1949, 1959) insights were highly influential, and helped prompt a generation of research focused on geographic variation in thermal behavior and physiology both within and among species.

Emerging from these early, formative studies was a conceptual debate regarding whether physiological evolution is generally "labile" or "conserved." On the one hand, an abundance of studies cemented what Bogert (1949) observed: ectotherms were often remarkably efficient at behaviorally homogenizing thermal variation, resulting in limited physiological divergence among close relatives (or even among distant relatives) and across environmental gradients (discussed in Hertz et al. 1983; Bodensteiner et al. 2021). This prompted a growing view that physiological evolution (including subcellular physiology; e.g., Ushakov 1964) was generally "static" owing to the homeostatic power of regulatory behaviors (e.g., Brown and Feldmeth 1971; Spellerberg 1972; Hutchison 1976; Hertz et al. 1983; Crowley 1985; Van Damme et al. 1990). On the other hand, other studies documented that thermoregulation and physiological stasis were far from universal outcomes. Many closely related ectotherms, for example, diverge in thermal habitat use and in thermal physiology (e.g., Ruibal 1961; Soulé 1963; Rand 1964; Brattstrom 1965; Corn 1971; Clark and Kroll 1974; Miller and Packard 1977; Hertz 1979; Hirshfield et al. 1980). Likewise, other studies found that lizards are behaviorally passive with respect to their thermal environments (e.g., Alcala and Brown 1966; Stebbins et al. 1967; Rand and Humphrey 1968; Ruibal and Philobosian 1970; Hertz 1974; Huey and Webster 1975).

These early comparative studies emerged in the prephylogenetic era (or in the nascently post-phylogenetic era), largely restricting investigators to more qualitative inferences about physiological "lability" or "conservatism" (Hertz et al. 1983). Nonetheless, many researchers rapidly embraced the comparative approach and, to the extent possible, employed phylogenetic methods to assess patterns of physiological evolution (e.g., Huey and Bennett 1987; Huey et al. 1989; Garland et al. 1991; Block et al. 1993; Walton 1993; Bauwens et al. 1995). Per these early studies, empirical support for the "conservatism" or "lability" hypotheses of physiological evolution was mixed and seemed to vary based on the specific traits and lineages examined (reviewed in Bodensteiner et al. 2021).

[3]To be clear, Bogert (1949) was not the first to articulate a case for behavior (or, plasticity, in a more general sense) being a factor in evolution, which can conceptually date back at least to Lamarck (1809), and certainly many others before the 20th century (e.g., Darwin 1859; Baldwin 1896; Morgan 1896).

Modern Conceptions of the Bogert effect

The early 21st century saw renewed interested in behavioral inertia, reflecting (at least in part) a major effort by Huey et al. (2003) to formalize Bogert's (1949, 1959) seminal observations about "behavioral inertia," and to provide a counter-perspective to the "behavioral drive" hypothesis (e.g., Mayr 1959, 1963; Gittleman et al. 1996).[4] The major leap afforded by Huey et al. (2003) was to connect the dots between regulatory behavior, selection, and evolution, and to articulate a hypothesis-driven framework for putting the Bogert effect to the test. Specifically, they proposed that testing the Bogert effect involves two general steps, which they illustrated using an example involving thermoregulation (while emphasizing that the effect should extend to any regulatory behavior). Their approach establishes two basic premises that should be met under the Bogert effect: (1) behavioral buffering is occurring, and (2) such buffering is associated with limited selection/evolution. These premises provide testable hypotheses for researchers interested in exploring the phenomenon in natural systems.

The first step involves testing whether organisms are behaviorally buffering environmental variation to maintain physiological homeostasis. To provide a test case, Huey et al. (2003) examined altitudinal variation in the thermal behavior of a Puerto Rican lizard, *Anolis cristatellus*. The approach they used (which follows Hertz et al. 1993) is well-described in their article, so I provide only a summary here. Briefly, to test whether regulatory behavior is occurring, Huey et al. (2003) compared field-measured lizard body temperatures to a distribution of available environmental (operative) temperatures, which describe the equilibrium temperature of an organism in the absence of behavioral regulation (Bakken 1992; Bakken and Angilletta 2014). Whether deviation between body and operative temperatures reflects behavioral homeostasis also requires knowledge of the thermal range that would optimize performance, as behavioral passivity will be homeostatic if, for example, the environment is already thermally optimal (Hertz et al. 1993; Camacho and Rusch 2017). Based on these considerations, the null hypothesis is that organisms are behaviorally passive with respect to their environments. Alternatively, organisms can actively regulate their core temperature through their behavior. In particular, behavioral thermoregulation occurs when field-measured body temperatures fall within the preferred thermal range more often than expected by chance, given available thermal conditions (Hertz et al. 1993).

[4]In this article, Huey et al. (2003) also coined the "Bogert effect" to describe behavioral inertia. Please note that the Bogert effect is different from "Bogert's rule" (which describes a positive relationship in ectotherms between external reflectance and solar radiation; see Gaston et al. 2009), although both do relate to Charles Bogert.

Behavioral passivity, by contrast, is supported when body temperatures generally overlap with the available thermal environment, which may or may not overlap with the preferred thermal range. These two opposing outcomes (and variation therein) can be quantified using metrics like thermoregulatory effectiveness, *E*, which describes the degree of behavioral buffering, given the local thermal environment and preferred thermal ranges of organisms (Hertz et al. 1993). Based on this null model approach, Huey et al. (2003) determined that *A. cristatellus* thermoregulates: body temperatures were more stable across elevation and across seasons than would be expected if these lizards were behaviorally passive with respect to the environment. Although Huey et al. (2003) focused on thermoregulatory behavior, they also emphasized that such a "null model" approach can be applied to a wide range of homeostatic behaviors.

The second step involves testing whether behavioral regulation is associated with more limited physiological divergence than would be expected in the absence of regulatory behavior. Given that performance is contingent on body temperature in ectotherms, field-measured body temperatures can be used to predict ecologically relevant measures, like sprint speed, informed by the thermal sensitivity of the trait (Huey 1983). Using data from *A. cristatellus*, Huey et al. (2003) predicted lizard sprint speed at low- and high elevation in the absence of behavior (i.e., based solely on operative temperatures from lizard models) and based on the observed body temperatures of the lizards. They found that behavioral thermoregulation in *A. cristatellus* was associated with faster and more similar sprint speeds at low- and high-altitude sites across seasons than would be expected if lizards were behaviorally passive with respect to temperature. Other approaches can also help researchers test whether behavioral buffering limits selection or phenotypic divergence. For example, selection can be measured directly by quantifying survivorship and reproductive success according to behavioral and physiological variation among individuals (e.g., Logan et al. 2014; Gilbert and Miles 2017).

Following publication of the conceptual synthesis by Huey et al (2003), interest in Bogert's (1949) ideas has flourished after several decades of relative doldrums[5] (Fig. 1), reflecting strong conceptual interest in the role of regulatory behavior in evolution (e.g., Ghalambor et al. 2007; Duckworth 2009; Doody and Moore 2013; Abram et al. 2017; Muñoz and Bodensteiner 2019). Many empirical studies support the notion that buffering behavior limits local adaptation (e.g., Castañeda et al. 2013; Muñoz and Losos 2018; Stellatelli et al. 2018). Nonetheless, the Bogert effect is not a universal outcome or a foregone conclusion (reviewed in Bodensteiner et al. 2021). In general, empirical support for the Bogert effect appears to be stronger when the thermal habitat facilitates thermoregulation (e.g., Lapwong et al. 2020), and in more mobile life stages (e.g., Carter and Sheldon 2020). Likewise, support for the Bogert effect also depends on the specific traits examined (Labra et al. 2009; Logan et al. 2019; Rozen-Rechels et al. 2020), as not all traits can be equally buffered against selection (Muñoz and Bodensteiner 2019). Southern rock agamas (*Agama atra*), for example, are highly effective thermoregulators when the environment is warm, but are less effective when the environment cools: correspondingly, physiological divergence is much more limited for traits on the upper end of the thermal performance curve in these lizards (Logan et al. 2019). Although the Bogert effect has been more often studied with respect to behavioral thermoregulation, several studies have found that other homeostatic behaviors, like hydroregulation, are likewise associated with strong behavioral buffering across environmental gradients (e.g., Farallo et al. 2018; Galindo et al. 2018; Rozen-Rechels et al. 2019).

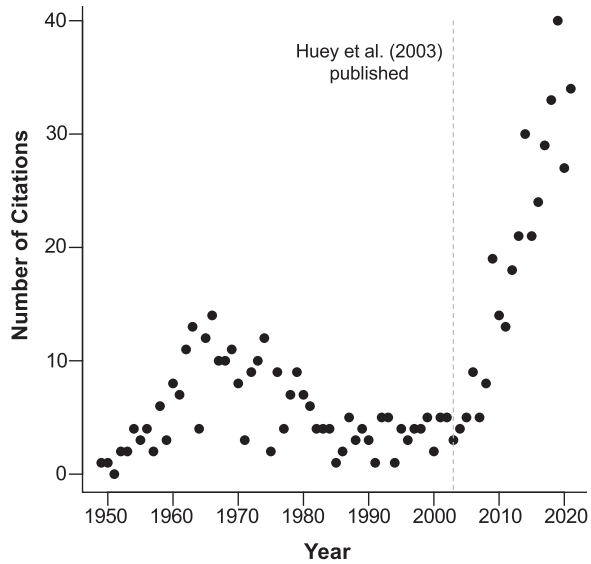

Figure 1. **Citations per year of Bogert (1949) since its publication. Following the publication of Huey et al. (2003) (year shown with the gray dashed line), citations of Bogert (1949) have greatly increased.**

The approach described by Huey et al. (2003) works quite well at microevolutionary scales (and this was their scale of focus), but becomes more challenging at macroevolutionary scales, which present the additional challenge of phylogenetic nonindependence (Felsenstein 1985; Harvey and Pagel 1991). Yet, one of the most provocative dimensions of the Bogert effect is its potential as a causal mechanism for long-term patterns of evolutionary stasis and uneven rates of evolution (Gingerich 1983, 2009; Wake et al. 1983). As Bartholomew (1964) put it, "each level

[5]Not mutually exclusive with this perspective is that, contemporaneously, modern comparative methods were emerging at a rapid pace, providing a more sophisticated toolkit for researchers.

[of biological integration] finds its explanation of mechanism in the levels below, and its significance in the levels above" (p. 8). When translated over long evolutionary time periods, behavioral buffering can be predicted to slow rates of evolution. Huey et al. (2003) appreciated this broader point, arguing that, under the Bogert effect, the "response to selection will be less than expected, slowing rates of evolution under natural conditions" (p. 362). Based on this notion, they postulated that behavioral inertia could help explain long-term patterns of evolutionary stasis (e.g., as captured by "Haldane's dilemma," Haldane 1949; Levinton 1988). Likewise, they highlighted how strong behavioral preferences, for example, through sensory biases in female choice, can also constrain phenotypic evolution (Huey et al. 2003). Below, I provide some conceptual background for macroevolutionary approaches, progress to date applying these approaches to questions about the Bogert effect, and avenues for future exploration.

RATES OF PHYSIOLOGICAL EVOLUTION UNDER THE BOGERT EFFECT

Under the Bogert effect, we can predict that the relative speed of physiological evolution is slower for thermoregulating lineages than for more behaviorally passive counterparts, and slower for traits that can be more readily buffered against selection than traits that cannot be as easily buffered (Huey et al. 2003; Logan et al. 2019; Muñoz and Bodensteiner 2019). Brownian motion (BM), or a "random walk," is the most commonly used model for analyses of trait evolution (Freckleton et al. 2002). This model describes a process of stochastic diffusion in which the amount of phenotypic variance among taxa increases proportionately with time (Felsenstein 1985). The evolutionary rate parameter, σ^2, describes the rate of the Brownian diffusion process, and is the metric often compared among traits and taxa (O'Meara et al. 2006; Thomas et al. 2006; Revell et al. 2008). Maximum likelihood approaches are commonly used to compare evolutionary rates among traits or lineages. Under such approaches, the likelihood of a model in which the rate of evolution (σ^2) is allowed to vary among traits or lineages is compared to the likelihood of a model in which σ^2 is constrained to be equal (e.g., O'Meara et al. 2006; Adams 2013). Under such a test, the "null hypothesis" would be that σ^2 is shared among all species (i.e., a single-rate model best explains physiological variation), and the alternate hypothesis is that allowing the evolutionary rate to vary among behavioral types improves the fit of the model (after accounting for the additional parameter).

A test of the Bogert effect using this approach could involve, for example, comparing rates of evolution among traits or lineages that exhibit different degrees of behavioral thermoregulation (Fig. 2). Among other factors, thermoregulatory capacity hinges on the spatial availability of thermal variation (Huey and Slatkin 1976; Tracy and Christian 1986; Hertz 1992; Sears et al. 2016): given sufficient thermal heterogeneity, many ectotherms are remarkably precise at targeting a narrow range of body temperatures (e.g., Díaz and Cabezas-Díaz 2004; Goller et al. 2014; Ortega et al. 2016; Muñoz and Losos 2018). In thermally homogenous environments, by contrast, thermoregulatory costs mount, limiting the feasibility or practicality of buffering behavior (Huey 1974; Sears and Angilletta 2015; Basson et al. 2017). Thermoregulatory costs also increase under strong predation pressure, and when it conflicts with other regulatory demands, like water balance (Huey and Slatkin 1976; Herczeg et al. 2008; Levy et al. 2011; Basson et al. 2017; Malishev et al. 2018). Correspondingly, we can predict that regulatory behavior will be stronger and that rates of physiological evolution will be slower in lineages that occupy "less costly" environments than their counterparts in environments that are "costlier" for thermoregulation (Fig. 2). Anole lizards, for example, vary in their use of thermoregulatory behavior: species found on Caribbean islands tend to thermoregulate more than species found on mainland Latin America (van Berkum 1986; Salazar et al. 2019). Thermoregulatory patterns among landmasses reflect, in turn, differences in predation/competition pressures and climatic variability afforded by their relative habitats (Greene 1988; Henderson and Crother 1989; Losos 2009; Velasco et al. 2018). Consistent with the Bogert effect, heightened thermoregulation in island anoles is associated with a threefold reduction in the rate of heat tolerance evolution when compared to mainland counterparts (Salazar et al. 2019).

Likewise, behavioral buffering should not be equally effective across the entire phenotype. Given that daytime environments are more thermally heterogenous than nighttime environments (Ghalambor et al. 2006; Muñoz and Bodensteiner 2019), thermoregulation might be more effective at buffering physiological traits on the upper end of the thermal performance curve (like the optimal performance temperature and heat tolerance) than physiological traits on the lower end (like cold tolerance), particularly in diurnal organisms (but see Huey and Bennett 1987). Correspondingly, upper thermal traits (e.g., heat tolerance, preferred temperatures) tend to evolve more slowly than lower physiological limits like cold tolerance (Muñoz et al. 2014; Gvoždík 2015; Von May et al. 2017; Qu and Wiens 2020). These studies fit into a broader picture of physiological variation in ectotherms. In general, upper physiological limits exhibit less geographic divergence, particularly in terrestrial organisms (e.g., Gaston and Chown 1999; Sunday et al. 2011; Brandt et al. 2020), a biogeographic pattern known as Brett's rule (Brett 1956; Gaston et al. 2009). Likewise, other studies have found higher phylogenetic signal in upper physiological limits than in lower limits (Grigg and Buckley 2013; Hoffmann et al. 2013; Gutiérrez-Pesquera et al. 2016; Von May et al. 2019; Bujan et al. 2020; but see Kellermann et al. 2012a,b), although phylogenetic

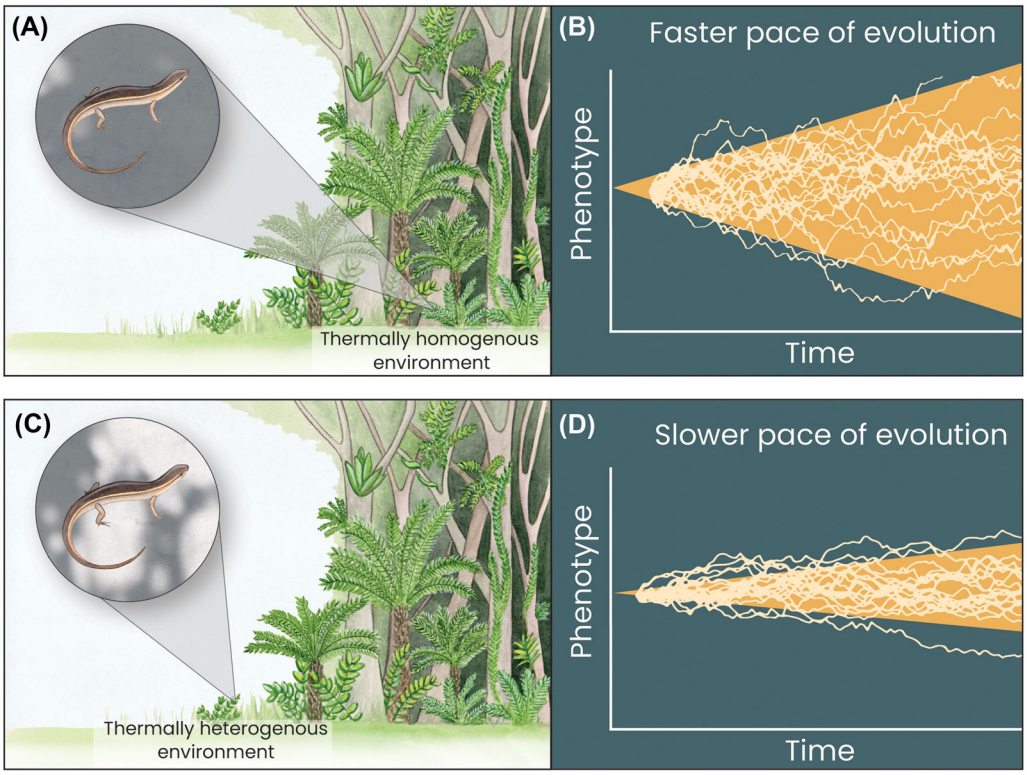

Figure 2. A visualization of the Bogert effect using reptile thermoregulation as an example. In panel A, a lizard behaviorally interacts with a thermally homogenous environment in closed-canopy forests (indicated by limited sun/shade patchiness in the inset). In turn, thermal homogeneity limits lizards' ability to behaviorally thermoregulate: when translated over long time periods, such lineages should be exposed to stronger selection on physiology, and exhibit faster physiological evolution (panel B). By contrast, more thermally heterogenous habitats, like forest edges or open habitat (panel C), provide greater opportunities for thermoregulation (indicated by greater sun/shade patchiness in the inset). When translated over long time periods, such buffering behaviors should limit exposure to selection and slow the rate of physiological evolution (i.e., the Bogert effect) (panel D).

signal (by itself) should be interpreted with caution. Similar amounts of signal, for example, can correspond to different underlying processes (Revell et al. 2008). Likewise, spatial proximity of closely related species can elevate phylogenetic signal in climate-related traits (Freckleton and Jetz 2009).

To be clear, many mechanisms beyond thermoregulation should influence this spatial pattern. Maximum environmental temperatures decline with altitude/latitude less sharply than minimum temperatures, although this also makes thermoregulation better poised to "flatten" upper thermal barriers across latitude and altitude (Ghalambor et al. 2006; Sunday et al. 2011; Buckley et al. 2013; Muñoz and Bodensteiner 2019). Physiological traits are subject to different underlying biochemical constraints, reflected in different patterns of adaptation that need not relate to behavior (Hochachka and Somero 1984; Johnston and Bennett 1996; Angilletta et al. 2010). Nonetheless, thermoregulation is an important determinant, as it disrupts the relationship between a species' physiology and its local environment. For example, heat tolerance and preferred temperatures are often higher in species occupying colder environments than their relatives in warmer environments (an example of counter-gradient variation), a pattern often thought to reflect a lower risk for overheating/performance costs via basking in cooler environments (Martin and Huey 2008; Fangue et al. 2009; Huey et al. 2009; Sunday et al. 2011; McElroy 2014; Llewelyn et al. 2017). Cold tolerance, by contrast, is typically more strongly correlated with the minimum temperatures that organisms experience (e.g., Addo-Bediako et al. 2000; Kimura 2004; Cruz et al. 2005; Clusella-Trullas et al. 2011; Sunday et al. 2011, 2012; Araújo et al. 2013), reflecting, among other factors, a more limited capacity to thermoregulate when the environment is coldest and more thermally homogenous, particularly at night and in winter (e.g., Sunday et al. 2011; Williams et al. 2015; Muñoz and Bodensteiner 2019). Comparative studies of physiological evolution are still limited, and many outstanding questions merit deeper consideration. For example, how do differences in geography, phylogenetic history, and microhabitat ecology (e.g., sun vs. shade use) contribute to rate differences in physiological evolution? How do differences in rates of physiological evolution correspond (if at all) to biogeographic patterns of diversity, like the latitudinal diversity gradient? Are

rates of physiological evolution faster in tropical regions, for example, reflecting tighter physiological barriers to dispersal (e.g., as captured by Janzen's hypothesis; Janzen 1967; Ghalambor et al. 2006; Polato et al. 2018; Sheldon et al. 2018)?

THE BOGERT EFFECT AND PHYLOGENETIC "LAGS" IN ADAPTATION

Although certainly useful, comparison of evolutionary rates is not the only means by which we can explore the Bogert effect. Intuitively, a species' physiology should reflect its local environment, but the strength of the trait-environment relationship can be modified through regulatory behaviors (Huey et al. 2003). In other words, under the Bogert effect, physiological phenotypes can be at least partially decoupled from their local environments. The SLOUCH (Stochastic Linear Ornstein-Uhlenbeck Comparative Hypotheses) approach (Hansen et al. 2008) provides a flexible environment for putting this idea to the test. The method uses an Ornstein-Uhlenbeck (OU) modeling framework to assess patterns and rates of trait adaptation to continuous predictor variables (Hansen et al. 2008). The OU model is a Brownian-like model characterized by the presence of one or more adaptive fitness optima (θ), with a rubber band parameter (α) drawing phenotypes toward the optima (Hansen 1997; Butler and King 2004).

To illustrate how the SLOUCH approach could be applied, we can consider the adaptation of heat tolerance (CT_{max}) to local environmental temperature in a lineage of organisms. Using an OU modeling framework, the approach involves estimating (and comparing) an "optimal regression" and an "evolutionary regression." The optimal regression describes the relationship anticipated under a scenario of full adaptation of CT_{max} to the thermal environment. The evolutionary regression, in contrast, describes the observed relationship between the trait and the predictor variable (in this scenario, the actual relationship between CT_{max} and the thermal environment). Under the Bogert effect, we can predict that the optimal and evolutionary regressions will differ in slope. In the absence of regulatory behavior, by contrast, we can predict a tighter association between the "evolutionary" and "optimal" regressions. Under the Bogert effect, correspondingly, the phylogenetic half-life of the model is bounded away from 0, representing "phylogenetic inertia," or a lag in trait adaptation to the predictor variable (Hansen et al. 2008). Greater differences in slopes of the evolutionary and optimal regressions are associated with longer phylogenetic lags in adaptation. Phylogenetic half-life ($t_{1/2}$) describes the amount of time necessary for a lineage to get halfway to its phenotypic optimum (Hansen et al. 2008; Münkemüller et al. 2015). In a manner analogous isotopic half-life, $t_{1/2}$ reflects the amount of time necessary for half of the phylogenetic signal in the data to "degrade" (be lost). Low $t_{1/2}$ (that is, $t_{1/2}$ approximating the youngest splits in the tree) indicates that phylogenetic signal in physiological variation is rapidly lost. By contrast, as $t_{1/2}$ approximates (or exceeds) the total length of the tree, trait evolution converges on BM (reflecting high phylogenetic signal in the trait data). Under the Bogert effect, we would expect the phylogenetic lag in physiological adaptation to be relatively high (i.e., high $t_{1/2}$ relative to total tree length). By contrast, the $t_{1/2}$ of the trait should degrade more rapidly when behavioral buffering weakens, reflecting adaptation to the local environment.

The model can perhaps be most powerfully applied when hypotheses about physiological adaptation in different types of organisms (varying, for example, in thermoregulatory capacity) or types of traits (varying in how readily they can be behaviorally buffered) are assessed. Given previous work showing that thermoregulatory behavior is more effective at buffering upper physiological limits than lower physiological limits, we can hypothesize that the Bogert effect should be associated with a longer phylogenetic lag in adaptation to the thermal environment for traits like the preferred temperature (T_{pref}) and heat tolerance (CT_{max}) than for cold tolerance (CT_{min}). In a recent study, Domínguez-Guerrero et al. (2021) put this idea to the test in phrynosomatids, a diverse lineage of diurnal, thermoregulating lizards from North and Central America. Indeed, $t_{1/2}$ is substantially higher (by millions of years!) for T_{pref} and CT_{max} than for CT_{min} (Fig. 3), supporting the notion that behavioral thermoregulation (which was estimated to be uniformly high in this lineage) differentially slows evolution among physiological traits. Nominally low phylogenetic half-life for CT_{min} suggests that, in this group of lizards, a species' cold tolerance more readily adapts to local thermal conditions than either T_{pref} or CT_{max}.

Yet, slower adaptation to the thermal environment in upper physiological limits is not universally the case. Liolaemid lizards from South America (Genus *Liolaemus*), by contrast, vary considerably in their thermoregulatory efficiency (ranging from behaviorally passive to highly precise thermoregulators; Marquet et al. 1989; Labra et al. 2001; Ibargüengoytía et al. 2010) and, in this lineage, the preferred temperature rapidly adjusts to the prevailing thermal conditions (i.e., low phylogenetic half-life) (Labra et al. 2009). Likewise, Kellermann et al. (2012a,b) found that phylogenetic half-life was relatively long for both heat and cold tolerance (and, surprisingly, even higher for CT_{min} than for CT_{max}) in *Drosophila* fruit flies. Therefore, much work remains in determining how (and why) broadscale patterns of thermal behavior and physiological adaptation vary across lineages, traits, and geography.

It is important to note that this OU modeling framework does not explicitly test the Bogert effect as such. Evolutionary patterns may differ for reasons other than regulatory behavior. Correspondingly, a strong hypothesis structure, good knowledge of the species' natural history, and acknowledgement of

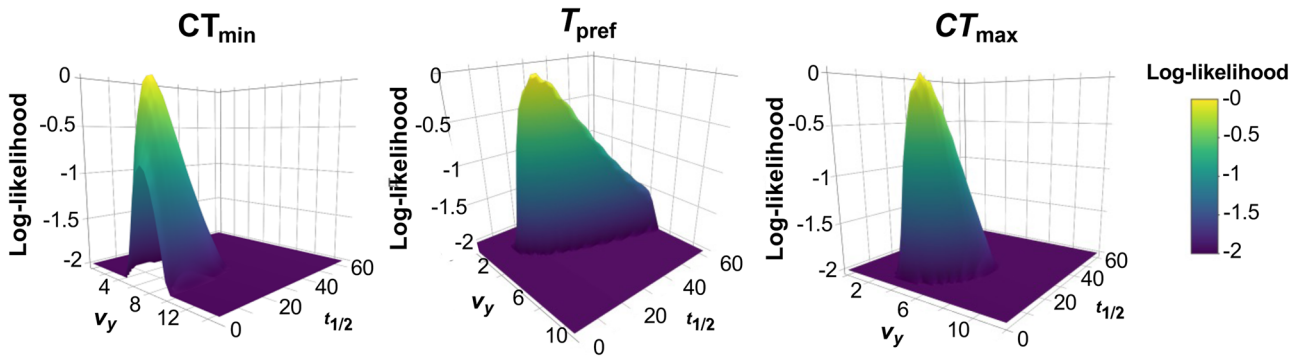

Figure 3. Patterns of adaptation in cold tolerance (CT_{min}), the preferred temperature (T_{pref}), and cold tolerance (CT_{max}) with respect to thermal environment. Likelihood support surfaces for the phylogenetic half-life ($t_{1/2}$) (in millions of years) and the stationary variance (v_y) for a regression of traits on mean annual temperature. V_y is a dispersion parameter describing the amount of variance about the optimum. The elevated area in each plot shows all points that are within two support units of the best estimate. Data reproduced from Domínguez-Guerrero et al. (2021)

alternative explanations are important considerations when applying this (and any) macroevolutionary approach (Uyeda et al. 2018). To properly interpret differences in phylogenetic half-life among species, prior knowledge of the regulatory capacities of different species in the analysis is needed. Under this schema, for example, one could test whether phylogenetic half-life in physiological traits is consistently higher in regulating species than in more behaviorally passive relatives. Another important consideration is that relatively complex models (like OU models) can be incorrectly favored over simpler models when the statistical power of the analysis is weak, for example, when species sampling is limited (Ho and Ané 2014; Cooper et al. 2016). There are a variety of simulation approaches available to assess the adequacy of one's phylogenetic data for more complex model fitting procedures (Beaulieu et al. 2012; Revell 2012; Pennell et al. 2014), and this is an important consideration for macroevolutionary studies of physiology.

EXTENDING THE BOGERT EFFECT: TESTING PREDICTIONS ABOUT PATTERNS OF PHENOTYPIC EVOLUTION

The discussion so far has largely focused on whether and how behavioral buffering should limit the rate of evolution. Although not directly predicted under the Bogert effect (sensu Huey et al. 2003), an additional dimension worth considering is how thermoregulation impacts evolution of the thermal sensitivity of performance. By this I mean that, by virtue of regulating their core temperatures, thermoregulation can influence both the pattern and the rate of physiological evolution. Optimality models can be used to predict the physiology of an organism given its behavior, its thermal environment, and underlying trade-offs and constraints (reviewed in Angilletta 2009). Given that higher temperatures accelerate chemical reactions (up until an intrinsic limit), the maximal performance of an organism often increases at higher optimal body temperatures (i.e., the "hotter is better" hypothesis; Hamilton 1973; Huey and Kingsolver 1989; Angilletta et al. 2010): this suggests that thermoregulation may often favor the evolution of warm-adapted, high-performance phenotypes. Likewise, thermoregulatory patterns fit into a broader series of considerations in physiological adaptation, like specialist-generalist trade-offs (Levins 1968; Angilletta et al. 2003, 2006; Angilletta 2009). In short, thermoregulatory behavior and the sensitivity of thermal performance are linked (Huey 1982; Angilletta 2009); correspondingly, different regulatory strategies may favor the evolution of different physiological phenotypes. To be clear, in this case I am not focusing on evolutionary rates, but rather on the potential for regulatory behavior to dictate the direction of physiological evolution. Huey et al. (2003) hint at this possibility: in their example of *A. cristatellus* performance, both low- and high-altitude lizard populations converged on the same emergent performance value (sprint speed), despite experiencing different thermal challenges (overly hot environments at low elevation and overly cold environments at high elevation).

On macroevolutionary scales, OU models provide a flexible framework for assessing how the pattern of phenotypic evolution might reflect different thermoregulatory strategies. As described above, OU models are characterized by the presence of one or more optimal values (θ) and selective pull (α) toward the optima (Hansen 1997; Butler and King 2004). Different optima, in turn, may have separate or shared evolutionary rates (σ^2) associated with them (O'Meara et al. 2006; Thomas et al. 2006). Testing whether and how trait optima vary based on regulatory patterns can be done by comparing how the additional of a behavioral parameter (e.g., thermoconformy vs. thermoregulation) alters the fit of different evolutionary models to the trait data, for example, in

the OUwie modeling environment (Beaulieu et al. 2012). Models vary in complexity, with a single-rate BM model being the simplest, and an OU model with varying optima, rates, and selective strengths among regimes (e.g., behavioral types) being the most complex. Each of these models can be fitted to the trait data, and support among models can be compared using AIC scores and weights (Burnham and Anderson 2002; Burnham et al. 2011). For example, if a single-rate BM model is sufficient to explain physiological variation among species, then there is no compelling support that behavior is driving differences in phenotypic evolution. Under the Bogert effect, by contrast, we might expect that regulatory behavior is associated with slower evolution and/or increases in trait optima (i.e., model fit is improved when a parameter differentiating species based on regulatory behavior is added). Simulation-based approaches can help researchers assess their ability to distinguish among models, given their phylogenetic data (e.g., Pennell et al. 2015).

Although still limited, progress to date suggests that differences in thermal behavior can be reflected by macroevolutionary shifts in the thermal sensitivity of performance. Rainforest skinks, for example, differ in basking behavior, with some species preferring cooler, shaded microclimates and others opting instead for forest edges or sun patches (Williams et al. 2010): the evolutionary optimum (θ) for heat tolerance is 6°C warmer for the basking skinks ($\theta_{open} = 43.0$°C) than for their shade-loving counterparts ($\theta_{shade} = 37.1$°C) (Muñoz et al. 2016). As mentioned above, body temperatures in Caribbean island anoles tend to be higher and more stable than those from their continental counterparts: not only is heat tolerance evolution slower on the islands, but the evolutionary optimum for this trait is also ~4°C warmer (Salazar et al. 2019). Likewise, viviparous lizards exhibit evolutionary reductions in the optimal phenotype for a number of thermal traits as compared to their oviparous counterparts, reflecting (among other features) a behavioral preference for cooler temperatures, regardless of ambient conditions (Domínguez-Guerrero et al. 2021). Although differences in phenotypic optima were not explicitly tested, a previous study of 94 *Drosophila* species by Kellermann et al. 2012a) found that fruit flies from wetter (i.e., more closed canopy) habitats exhibited lower heat tolerance than species from hotter (i.e., more open) habitats. As described above, thermoregulatory capacity is often more limited in closed-canopy habitats (Fig. 2), which are generally more spatially homogeneous thermal environments than edge/open habitats (e.g., Huey 1974; Hertz 1992; Sears et al. 2016). Correspondingly, in many ectotherm taxa, thermal physiology can relate to canopy use, with species using open/edge habitats often exhibiting higher core temperatures and heat tolerances than close relatives using more closed canopy habitats (e.g., Ruibal 1961; Rand 1964; Kleckova et al. 2014; Muñoz et al. 2016).

As a general caveat, hypothesis-testing frameworks require a priori behavioral assignations (which by default must also be discretized). Hypothesis testing approaches, however, can also erroneously associate predictors with specific evolutionary outcomes, particularly if the focal evolutionary event is rare (Uyeda et al. 2018). A separate approach could involve more agnostic searches for evolutionary shifts in phenotypic optima (sometimes termed "phylogenetic natural history"; Uyeda et al. 2018). Of utility in this regard is the R package bayou (Uyeda and Harmon 2014): this is a Bayesian method that employs reversible-jump Markov chain Monte Carlo (MCMC) to fit multi-optima OU models to estimate the location, direction, and magnitude of adaptive phenotypic shifts in θ and σ^2 across the phylogeny, and which has already been applied to recover macroevolutionary shifts in physiological characters (e.g., Uyeda et al. 2017). Whether through hypothesis testing (e.g., OUwie) or hypothesis "discovery" (e.g., bayou), connecting transitions in the evolutionary optima (θ) in physiological phenotypes presents a promising, but little examined, dimension of the Bogert effect, and may help explain biogeographic patterns of physiological variation like Brett's rule (e.g., Gaston et al. 2009). Many core questions remain unanswered. For example, how do optimal phenotypes vary across geography, lineages, and according to microhabitat use? Are shifts to higher evolutionary optima necessarily associated with slowdowns in evolutionary rate, or can these phenomena be decoupled?

The Multidimensional Impacts of the Bogert Effect (and What about Behavioral Drive?)

Until now, I have almost exclusively focused on the role of regulatory behavior in physiological evolution (particularly thermal physiological evolution). But, because of the interaction between regulatory behaviors and body size, shape, and color (among other variables), behavior does not operate in isolation from other phenotypic dimensions (Bogert 1949; Huey et al. 2003). Through their behavior, organisms can modulate their radiative, conductive, and convective environments, but their morphology will help dictate the emergent physiological properties of those interactions (Christian et al. 2006; Kingsolver and Huey 2008). Coloration, for example, modulates rates of heat gain/loss and UV absorption (Porter 1967; Porter and Norris 1969; Gates 1980; Clusella-Trullas et al. 2007). In pierid butterflies, for example, wing coloration (particularly the relative amount of melanin) and thermoregulatory behavior are functionally linked. Experimental manipulation of the amount of dark pigment in butterfly wings, for example, prompts shifts in flight activity and thermoregulatory posture; even the side of the wing on which pigmentation

is found matters for thermal behavior (Kingsolver 1987). Cowles and Bogert (1944) certainly appreciated this broader point, and focused much attention on how size, shape, and color impact thermal relations (also discussed in Bogert 1949, 1959). Correspondingly, in order for an organism's behavioral decisions to be fine-tuned to its environment, they must also be calibrated against other phenotypic dimensions that impact its physiology.

Not only are morphology, physiology, and behavior in constant dialogue, but the Bogert effect itself might extend into nonphysiological dimensions. In their original formulation, Huey et al. (2003) noted that buffering behaviors can (and often do) involve shifts in resource use. For example, thermoregulation in colder environments often occurs by switching to different types of perches in more open habitats (Rand 1964; Huey and Webster 1976; Adolph 1990; Refsnider et al. 2018). In turn, shifts in microhabitat use are often associated with changes in morphology, performance, and diet, among many other features (Losos and Sinervo 1991; Araújo et al. 2011). Likewise, organisms often make behavioral decisions for microhabitat use that are constrained by competing demands (like temperature, moisture, and salinity), illustrating the multidimensional considerations relevant for a given behavior (e.g., Reiser et al. 2017; Farallo et al. 2018, 2020; Malishev et al. 2018; Sannolo and Carretero 2019; Rozen-Rechels et al. 2020). In lungless salamanders, for example, the use of warm microclimates decreases in drier environments, reflecting a preference for temperature-moisture combinations that minimize evaporative water loss (Farallo et al. 2020). To the extent that resources are shared across niche dimensions, a single behavior might, therefore, have both homeostatic and nonhomeostatic effects for different phenotypic dimensions (Lewontin 1983; Levins and Lewontin 1985; Huey et al. 2003). Correspondingly, the same regulatory behavior that facilitates the Bogert effect for some traits may have the opposite evolutionary effect on other traits.

Anole lizards from the Caribbean island of Hispaniola provide a clear example of this phenomenon. At low elevation, *Anolis cybotes* (a member of the trunk-ground ecomorph; Losos 2009) mostly uses vertical perches, especially tree trunks in partially shaded habitats, like along forest edges (Schwartz 1989; Wollenberg et al. 2013; Muñoz and Losos 2018). Their close relatives at high elevation (*Anolis armouri* and *Anolis shrevei*), by contrast, eschew tree trunks, opting instead to perch on boulders, particularly in open habitats (Hertz and Huey 1981; Wollenberg et al. 2013; Muñoz et al. 2014). This switch in structural supports confers a distinct thermoregulatory advantage: although nearly all arboreal perches at high elevation are below these lizards' preferred thermal range, boulders are much more often optimally warm, facilitating thermoregulation and precluding physiological divergence in all traits examined except for CT_{min}, as high-elevation lizards are more cold tolerant (Hertz and Huey 1981; Muñoz et al. 2014; Muñoz and Losos 2018). As described above, behavioral buffering is often more limited for cold tolerance than for other thermal traits (Muñoz and Bodensteiner 2019). While facilitating the Bogert effect, this same perch switch is also associated with morphological evolution, namely, specialization in skull and limb dimensions for a boulder-dwelling, or saxicolous, lifestyle (Fig. 4). This pattern (regulatory behavior influencing both physiological and morphological evolution) may be generalizable: behavioral switches to preferred climatic conditions are common, and often involve switches in microhabitat use (e.g., Kingsolver 1983; Sømme 1989; Huey et al. 2003; Merrill et al. 2008; Ashton et al. 2009; Harvey and Weatherhead 2010; Farallo and Miles 2016). Correspondingly, the Bogert effect may often involve, as a correlated effect, evolution in other phenotypic dimensions.

As described in the *Introduction*, the notion that behavioral shifts—like the switch from tree trunks to boulders described above—can promote (rather than restrain) evolution is known as "behavioral drive." This concept has a rich conceptual history, strong empirical support, and, if anything, might be considered the more "classic" view on the role of behavior in evolution (Schmalhausen 1949; Mayr 1959, 1963; Wyles et al. 1983; Huey et al. 2003). By enabling organisms to either exploit new resources within their ancestral habitats or enter new habitats altogether, behavior can expose organisms to selection, in turn spurring adaptive evolution (Mayr 1963; Wyles et al. 1983; Plotkin 1988; Wcislo 1989; Sol et al. 2005, 2008). To be clear, these two phenomena—behavioral drive and behavioral inertia—are not mutually exclusive. Rather, as illustrated above, through shared ecological resources that span phenotypic dimensions, they may represent different sides of the same coin. Rather than determine whether a behavioral feature is associated with faster or slower evolution in some phenotypic dimension, we should anticipate more multidimensional interactions. More broadly, links between behavioral drive and inertia suggest that related phenomena, like "niche conservatism" and "niche divergence" (reviewed in Losos 2008; Wiens et al. 2010), might likewise be interconnected. In the case of the anoles described above, climatic preferences among anoles were retained (conserving several aspects of thermal physiology across environmental gradients) at the expense of divergence in structural niche use (with implications for morphological specialization). To the extent that resources are shared across niche dimensions, conservatism in one niche dimensions may impinge on selective pressures in other niche dimensions (Levins and Lewontin 1985; Huey et al. 2003). Climatic niche conservatism is a widely observed pattern in biological systems (reviewed in Wiens et al. 2010). How axis specific are patterns of niche conservatism, and how generalizable are they across lineages and geography? Should stronger conservatism in one niche dimension be associated with stronger niche

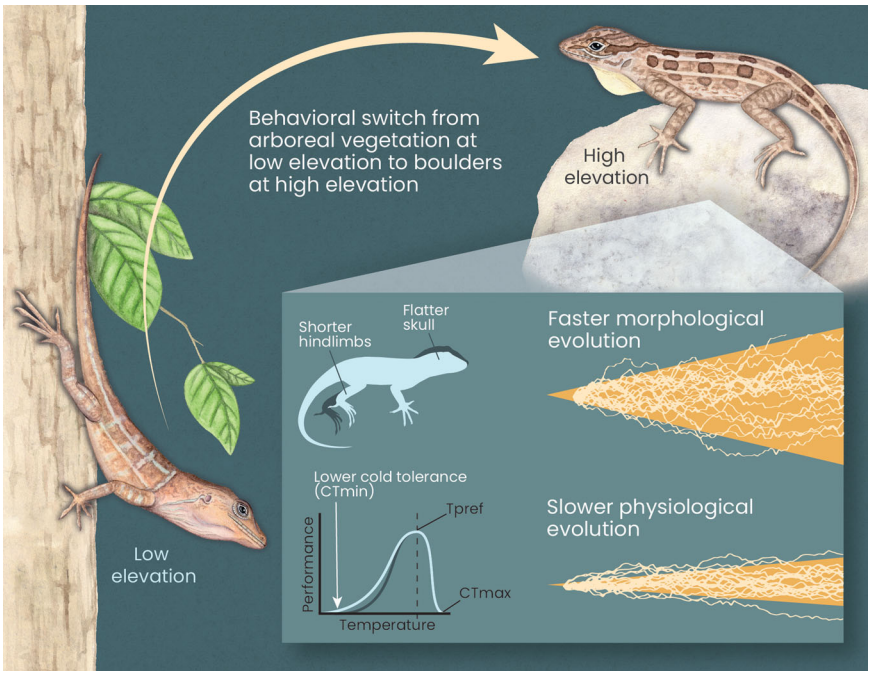

Figure 4. **Connections between the Bogert effect and behavioral drive are illustrated using anole lizards from Hispaniola as an example. At high elevation, arboreal perches (the ancestral structural niche) are too cold for thermoregulation to be effective. Correspondingly, high elevation anoles behaviorally shifted to perch on boulders. This perch switch facilitates thermoregulation, and is associated with limited divergence across elevation in several physiological traits. Although this perch switch shields lizards from selection on some aspects of thermal physiology, it does so at the expense of exposing organisms to selection on morphology, in turn impelling evolution. In particular, high-elevation lizards exhibit dorsoventrally compressed skulls and shorter hindlimbs (shown with the light blue silhouette). A single behavioral shift, therefore, can both accelerate and slow evolution. A male *Anolis cybotes* (low elevation) and a female *Anolis shrevei* (high elevation) are shown in the graphic. Graphic based on Muñoz and Losos (2018)**

divergence along others? Investigations of behavior and niche evolution should embrace these complex interactions, and anticipate "the vectors and tensions that link these multidimensional roles" (p. 363) (Huey et al. 2003).

The Bogert Effect and Speciation

Behavior is often viewed as a motor for speciation by driving phenotypic divergence, in turn generating reproductive barriers, for example, through shifts in resource use, migration, mating patterns, or other isolating mechanisms (Mayr 1963; Lande 1981; Price et al. 2003; Uy et al. 2018). But, if behavioral drive can facilitate speciation, then perhaps behavioral inertia can slow it down. By homogenizing environmental variation, behavioral buffering can limit local adaptation across broad geographic scales (Buckley et al. 2015; Enriquez-Urzelai et al. 2018). Correspondingly, thermoregulation might be generally associated with enhanced gene flow and limited genetic divergence among populations (Huey et al. 2003). This notion, however, remains little tested. In a study of *Anolis cristatellus* (a thermoregulating Puerto Rican anole lizard), McElroy (2018) found that, surprisingly, genomic differentiation across environmental transects was strong in *A. cristatellus*. Nonetheless, genetic variation correlated more strongly with precipitation than with temperature, suggesting that hydric physiology likely diverges among populations of *A. cristatellus* even as thermal buffering limits variation in thermal physiology. Therefore, although thermoregulation can potentially limit thermal variation and facilitate gene flow with respect to thermal barriers to dispersal, other axes of environmental divergence may not be so readily buffered (or, through inertia-drive connections, behavioral buffering in one dimension may require exposure along another; Muñoz and Losos 2018). Whether enhanced thermoregulation is generally associated with more limited genomic divergence than behavioral passivity is open for deeper exploration. Such tests might be most compelling in a comparative framework, for example, by contrasting genetic variation among species that vary in thermoregulatory behavior across shared environmental gradients. For example, Hertz and Zouros (1982) found less genetic variability in a thermoregulating species of anole (*Anolis roquet*) than in a more behaviorally passive counterpart (*Anolis gundlachi*).

Although explicit tests of this prediction under the Bogert effect are limited, there is a broader literature assessing genetic divergence across environmental clines that is relevant for

consideration. Under Janzen's hypothesis, for example, reduced seasonal temperature variation in the tropics should result in more limited thermal overlap across elevational bands than for comparable shifts on temperate mountains (Janzen 1967; Ghalambor et al. 2006; Sheldon et al. 2018). Correspondingly, physiological barriers to dispersal should be stronger (or "higher") for tropical organisms than for their temperate counterparts. In a major study of tropical and temperate insects, Polato et al. (2018) found that, indeed, tropical clades exhibit greater physiological specialization, lower rates of dispersal, greater population structuring across elevation, and faster rates of speciation than their temperate counterparts. Greater thermal heterogeneity within sites and shared thermal overlap among sites, like those afforded by temperate environments, is a key substrate for thermal buffering across environmental gradients: correspondingly, regulatory behaviors may contribute to the patterns of higher gene flow and greater dispersal observed in temperate lineages (although regulatory behavior was not compared in the study). Future investigations could involve comparing, for example, patterns of genetic divergence in temperate and tropical organisms that vary in thermal behavior. Are patterns of genetic divergence across elevational gradients similar for tropical and temperate lineages if tropical species thermoregulate, or are tropical lineages nonetheless constrained by steeper physiological barriers for dispersal? Within temperate or tropical regions, do patterns of genetic divergence align with regulatory behavior, or are patterns dictated most strongly by environmental variation?

Behavioral shifts are often associated with faster speciation. In birds, for example, bursts of song evolution (Mason et al. 2016) and enhanced behavioral innovation (Nicolakakis et al. 2003) are associated with faster rates of speciation. When extrapolated across long timescales, rates of speciation might correspondingly be lower in thermoregulating lineages, for example, than in more thermally passive counterparts. Alternatively, given that thermal variation represents just one major ecological pressure (and that buffering is not equally effective among trait dimensions), signatures of the Bogert effect on speciation might be weak. Is there a directionality to the role of behavior on speciation? Is behavioral drive sufficient to accelerate speciation due to the abrupt nature of reproductive isolation that can be imposed by behavioral shifts? By contrast, is strong regulation in some physiological dimension less likely to inhibit speciation because it could easily be associated with weak regulation in other physiological dimensions?

Multiple approaches exist for estimating and comparing rates of speciation among lineages, but largely employ state-dependent speciation and/or extinction models to test the effect of a discrete character on evolution. Among these, Hidden State-Dependent Speciation and Extinction models (HiSSE; Beaulieu and O'Meara 2016) are especially promising: in these models, an unobserved "hidden" character is introduced to the model, reducing the risk of erroneously attributing all rate variation to the character of interest, like thermoregulatory behavior (rather than a correlated factor). There are caveats, of course, to such approaches. Thermoregulation (like any regulatory behavior) reflects a response continuum, but evolutionary approaches rely on discretized variables, which requires users to categorize species as "regulating" or "nonregulating" (a somewhat arbitrary distinction). Sliding windows for discretized categories can help assess the robustness of any observed patterns to the cutoffs employed. Given the hypothesized effect of behavior on species generation rather than species loss (e.g., Nicolakakis et al. 2003), estimation of extinction rates may not be as relevant and, more practically, inherently difficult in extant lineages (Louca and Pennell 2020): correspondingly, such tests might be most compelling when limited to speciation rate (rather than diversification rate), although this necessarily restricts the inference space of one's conclusions. Whether on shallower or deeper timescales, the connection between buffering behavior and speciation remains a persistent gap, and open for deeper exploration.

Concluding Thoughts

The original (and enduring) vision of SSE was to foster cross-disciplinary study in evolutionary biology. In this regard, the seminal contributions of Cowles and Bogert (1944) and the key follow-up studies by Charles Bogert (1949, 1959) brought this vision to life: their prescient ideas linked behavior, morphology, physiology, and evolution, and helped spark an entire generation of research, particularly among comparative physiologists. More than half a century later, Huey et al. (2003) revisited and added flesh to these pioneering ideas by developing a hypothesis-driven framework, and a new name (the "Bogert effect"). The perspective by Huey et al. (2003) helped galvanize renewed interest in the inhibitory role of behavior in evolution. Nonetheless, empirical progress to date has largely centered at the microevolutionary scale (comparing populations within species) or through macroevolutionary comparisons with relatively few species. Robustly linking the Bogert effect to macroevolutionary patterns of diversity and rates of evolution remains an outstanding gap in the literature, despite many authors coalescing around this perspective (e.g., Huey et al. 2003; Duckworth 2009; Muñoz and Bodensteiner 2019; Bodensteiner et al. 2021). Likewise, although the phenomenon has been most frequently studied in the context of thermoregulatory behavior, it also applies to any homeostatic behavior, with many avenues ripe for deeper exploration.

The recent explosion of large-scale phylogenies and more sophisticated comparative methods position the community such that the data and the computational toolkit can finally catch up to classic ideas. But, for the rubber to really hit the road, large-scale

behavioral and physiological trait databases must also become available. Although advances in imaging (e.g., Yopak et al. 2018) and bioinformatic pipelines (e.g., Macleod 2017) have streamlined the collection and analysis of morphological detail, gathering physiological data remains time-intensive and laborious. Although data collection certainly remains the rate-limiting step for studies of the Bogert effect, there is no substitute for good natural history and field ecology, and these were crucial catalysts for the original ideas about behavioral inertia. And, to be sure, large-scale physiological databases are emerging (e.g., Sunday et al. 2011; Uyeda et al. 2017; Qu and Wiens 2020), and many more are certain to come.

Although the Bogert effect has historically been the domain of comparative physiologists (and, one could argue, that behavioral drive has largely been studied by comparative morphologists), I think the phenomenon is ready to go more mainstream. Behavior, morphology, and physiology are locked together in a delicate evolutionary dance, no part divisible from the rest. We cannot fully understand the physiology of regulatory behaviors, for example, if we do not also understand organismal morphology. More to the point, behaviors do not occur in selective vacuums, so that any behavioral adjustment with respect to one aspect of the phenotype can cause evolutionary ripples (or waves) in others. Multidimensional and macroevolutionary studies can provide a window into the generalizability (and limitations) of the Bogert effect, and provide insightful linkages between behavior, phenotypic diversity, niche evolution, and speciation.

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AUTHOR CONTRIBUTION

MMM was involved in all aspects of analysis and writing.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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