ARTICLES

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Mosquito Bite-induced Color Change in Chameleon Skin

For chameleons, changing color plays a significant and complex role in their daily lives by expressing communication cues. In male-male contests, rapid color change can convey to competitors that the individual is highly motivated to protect their territory and initiate combat (Ligon and McGraw 2018). Color-changing communication is also involved in mate courtship and female receptiveness. Chameleons can also change color to express stress, as well as to thermoregulate and hide from potential predators (Best 1968; Stuart-Fox and Moussalli 2009; Teyssier et al. 2015; Duarte et al. 2017).

While we now have a better understanding of the structural mechanism of coloration in chameleons, signals leading to alterations in coloration and patterning have not been directly studied in Chamaeleonidae and are considered to be driven by neuronal and/or hormonal signals (Bagnara et al. 1968; Bagnara and Matsumoto 2006; Teyssier et al. 2015). Color change can be achieved by modulation of chromatophore orientation and density, as well as by melanosome movement within the dermal chromatophore unit. There are four types of chromatophores identified across chameleons: melanophores, xanthophores, erythrophores, and iridophores (Teyssier et al. 2015). Within melanophores, motor kinesin carries melanosomes across the cell via actin myofilaments that make up the cytoskeleton (Best 1968; Bagnara and Matsumoto 2006; Ligon and McCartney 2016). Xanthophores and erythrophores express yellow and red color pigmentation, respectively. Chameleons have two thick layers of colorless iridophores, which bracket the other chromatophores (Teyssier et al. 2015). Iridophores are controlled by changing the distance of guanine crystals. In the superficial iridophore layer, changing the crystal distance reduces the amount of light reflected and causes the exaggeration of the interlaced yellow and red pigmentation among adult male chameleons.

PABLO GARCIA
Department of Integrative Biology, University of South Florida, Tampa, Florida 33620, USA; e-mail: pabloalejandrogarciajr@gmail.com
RAUL E. DIAZ JR.
Department of Biological Sciences, California State University Los Angeles, Los Angeles, California 90032, USA
CHRISTOPHER V. ANDERSON
Department of Biology, University of South Dakota, Vermillion, South Dakota, 57069, USA
TOVO M. ANDRIANJAFY
Department of Medical Entomology, University of Antananarivo, Antananarivo 101, Madagascar
LEN DE BEER
Eden Reforestation Projects, Antananarivo, 101, Madagascar
DEVIN A. EDMONDS
Department of Natural Resources and Environmental Sciences, University of Illinois Urbana-Champaign, Urbana, Illinois 61801, USA
RYAN M. CARNEY
Department of Integrative Biology, University of South Florida, Tampa, Florida 33620, USA; e-mail: ryancarney@usf.edu

Citizen science, also known as community science, can be useful for monitoring biodiversity, including chameleons and mosquitoes (Carney et al. 2022; Sousa et al. 2022). iNaturalist is the largest global citizen science platform and represents a social network where six million users have contributed more than 150 million observations of biodiversity. During an ongoing iNaturalist campaign targeting mosquito vectors in Africa (Carney et al. 2023), we discovered that a citizen scientist (LdB) in Madagascar documented two probable *Culex* sp. mosquitoes feeding on a previously sleeping endangered chameleon, *Calumma* (*C.*) *globifer* (Globe-horned Chameleon; Fig. 1A). At least one of the mosquito bites appears to have induced a localized melanic color change, emanating radially from where the proboscis pierced the chameleon's skin. This citizen science-based observation prompted this research group to develop a hypothesis that a yet to be identified compound in *Culex* saliva is involved in the color change, with its action either being through neuronal or hormonal modulation locally. Herein we present preliminary work aiming to test whether the presence of the *Culex* next to the black spots on the chameleons was purely correlative, and also take an initial step toward identifying a possible pathway for the formation of this black spot.

Methods and Results

iNaturalist Image Searching.—We initiated searches on iNaturalist at the family level for chameleons (Chamaeleonidae). Scrolling through images, we systematically identified cases where mosquitoes were observed feeding on the chameleons. Upon searching for similar mosquito bite-induced color change in chameleons, we found an iNaturalist observation of other probable *Culex* sp. mosquitoes feeding on a different endangered chameleon species, *Furcifer* (*F.*) *minor* (Lesser Chameleon) in Madagascar. Many atypical black spots on the chameleon are visible and likely caused by other mosquitoes having already fed (Fig. 1B). Similarly, a black spot was induced by a probable *Culex* sp. mosquito feeding on a sleeping juvenile

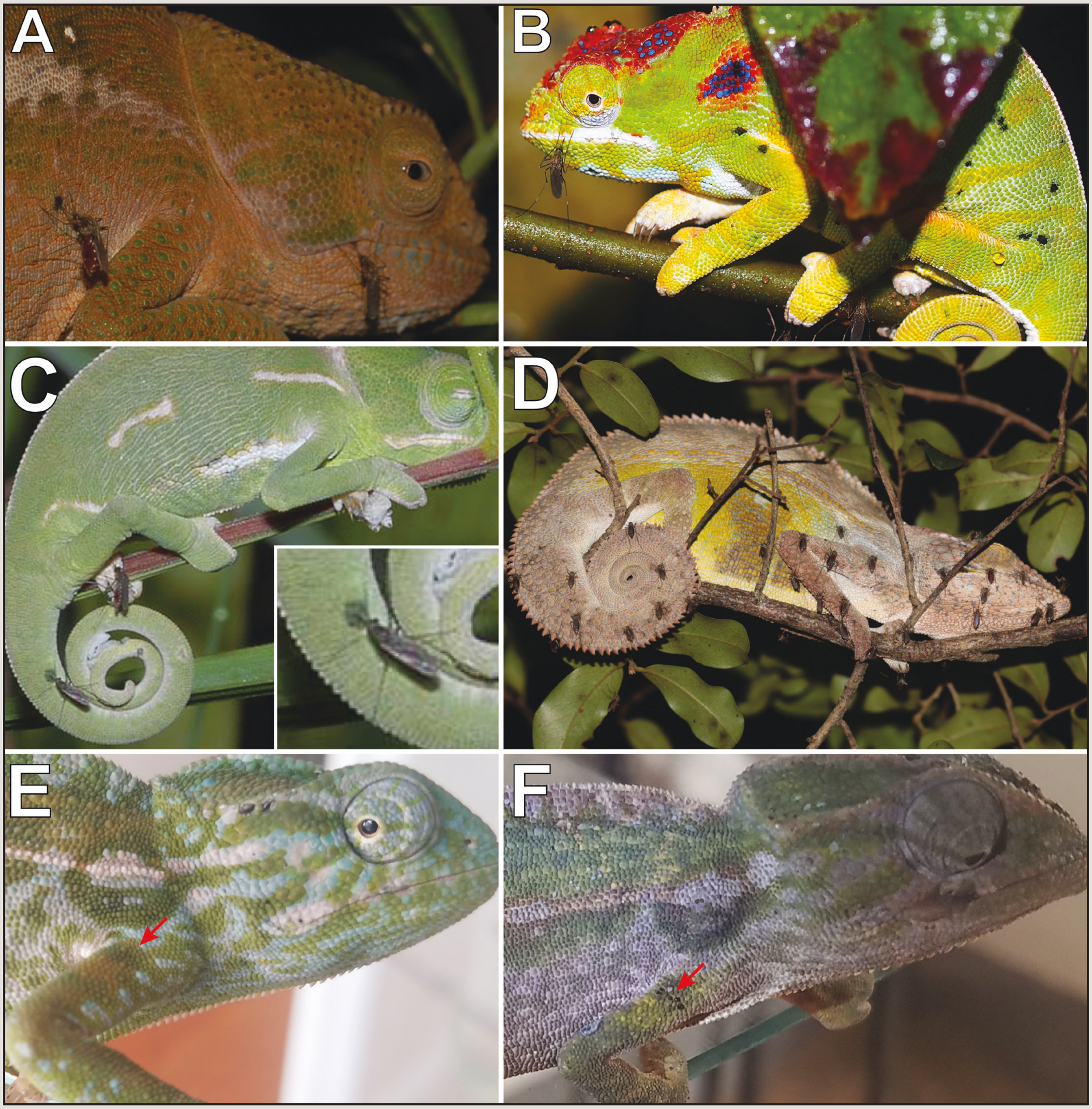

Fig. 1. Probable *Culex* spp. mosquitoes observed feeding on sleeping chameleons, November 2022 to January 2023: A) two mosquitoes feeding on a juvenile *Calumma globifer* (Globe-horned Chameleon). One mosquito is feeding near the chameleon's mouth (https://www.inaturalist.org/observations/141763778); B) three mosquitoes feeding on the mouth and foot of an adult female *Furcifer minor* (Lesser Chamelon). Small black spots on the body may represent prior mosquito bites (https://www.inaturalist.org/observations/146335596); C) two mosquitoes feeding on a juvenile *Chamaeleo calyptratus* (Veiled Chameleon), with one inducing a black spot on the tail; D) 33 mosquitoes feeding on a sleeping *Furcifer nicosiai* (Nicosia's Chamelon). At least four mosquitoes are feeding near or in the chameleon's mouth (https://www.inaturalist.org/observations/40691046); E, F) male *Furcifer lateralis* (Carpet Chamelon) before and after undergoing female mosquito blood meal experiments. Red arrow points to black spots that developed after blood meal experiments.

Chamaeleo (*Ch.*) *calyptratus* (Veiled Chameleon) in Florida, as seen in photos shared via a reptile photography Facebook group (Fig. 1C). Approximately 33 probable *Culex* were also observed feeding on a sleeping endangered *F. nicosiai* (Nicosia's Chameleon) in Madagascar (Fig. 1D). While we found six other examples online of mosquitoes feeding on various chameleon species, black dots were not observed because the bite locations were obscured or the mosquitoes were not fully engorged; presumably, a longer duration of blood feeding is necessary to induce color change.

Lab Experimental Procedures.—To further investigate the mosquito bite-induced melanic color change in chameleons, we

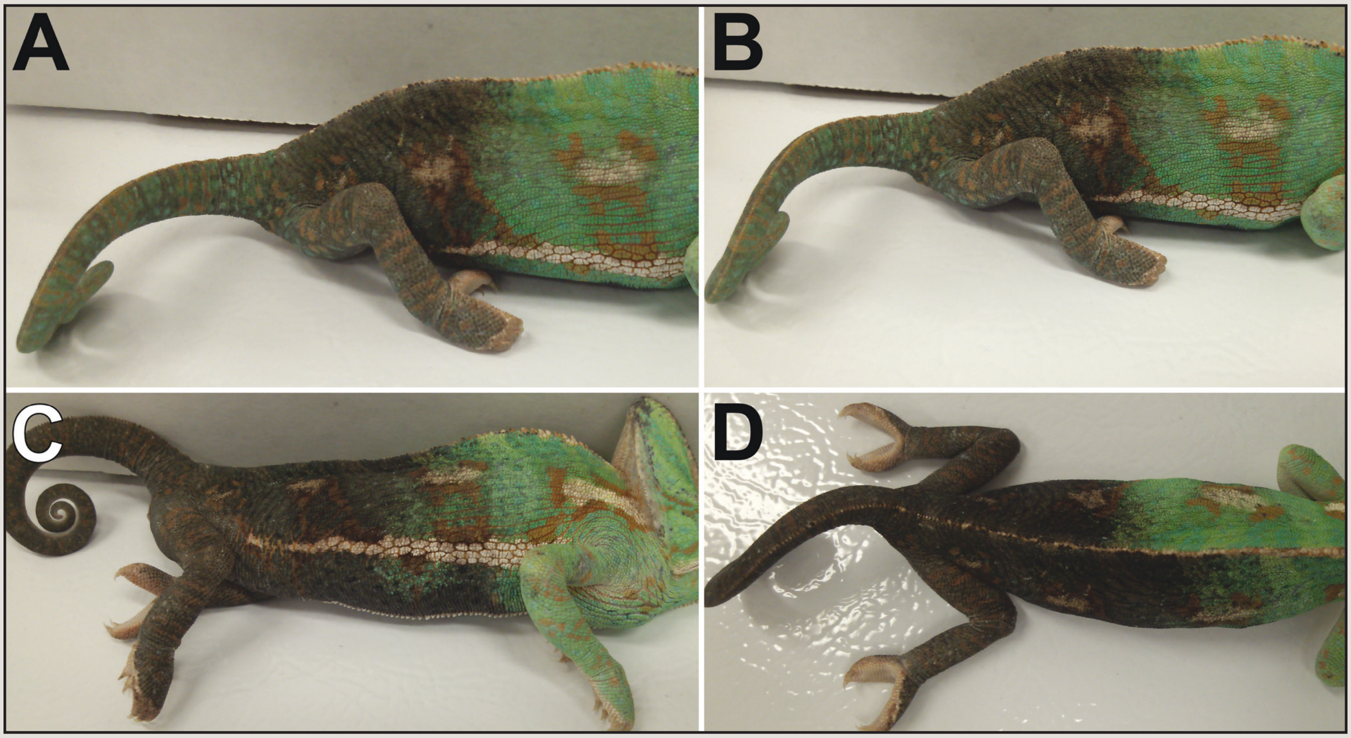

Fig. 2. A–D) Temporal series of photos spanning 3 min following abdominal intraperitoneal injection of tricaine in *Chamaeleo calyptratus* (Veiled Chameleon). The dark color spreads caudally and cranially from the injection site and differs bilaterally as seen in the dorsal view (D).

conducted controlled lab experiments in Madagascar. Male and female specimens of *F. oustaleti* (Malagasy Giant Chameleon; N = 2; 27–40 cm SVL) and *F. lateralis* (Carpet Chameleon; N = 4; 18–22 cm SVL) were exposed to 5–10-day-old female *Aedes* (*Ae.*) *albopictus* (N = 25) and *Culex* (*Cx.*) *quinquefasciatus* (N = 25). These mosquitoes were fasted for 24 h in separate cages. Subsequently, bloodmeal experiments began by introducing an adult chameleon into each cage containing the fasted mosquitoes. Pictures of the chameleons were taken before and after the bloodmeal to determine if black spots appeared after mosquito bites. In addition, each specimen had their skin pierced with a hypodermic needle and observed to determine if mechanical puncture alone could cause a melanic color change. Notably, in this experiment, while we observed the development of black spots at mosquito bite locations in each *F. lateralis* specimen (e.g., Fig. 1E, F), we did not observe a similar color change after blood meal experiments in *F. oustaleti*. Furthermore, no black spots appeared after hypodermic needle puncture in either species. Thus, we can conclusively show, in a controlled lab setting, that bites from species of *Aedes* and *Culex* cause a melanic color change in *F. lateralis*, but not in *F. oustaleti*. Following the intraperitoneal injection of MS-222 (tricaine methanesulfonate) for euthanizing veiled chameleons (Conroy et al. 2009; La Sierra University IACUC #LS01, for an unrelated project), one of the authors (RED) noticed a radial melanization from the site of injection which in retrospective comparison mimics (at a much larger scale) the local melanization identified after mosquito feeding in Malagasy chameleons. Benzocaine and its derivatives (such as MS-222) are known to affect sodium channel conductance and thus block action potentials (Butterworth and Strichartz 1990; Bai et al. 2003; Ramlochansingh et al. 2014). Thus, one hypothesis for the mechanism of melanization may be through the interruption of neural signaling to pigment cells, rather than through an endocrine mechanism.

Discussion

Our experimental evidence supports the mosquito bite etiology of the color change that was first observed by the citizen scientists, with the caveat that further research is required to determine the exact mechanism(s). Mechanisms that control chameleon color change could involve neural and/or endocrine signaling, but there has been limited research on both pathways (Hogben and Mirvish 1928; Okelo 1986; Bagnara and Matsumoto 2006; Teyssier et al. 2015). Potentially, one or more proteins within mosquito saliva disrupt these mechanisms, making the melanin pigments visible as a black dot radiating from the bite site. However, much is still unknown about mosquito saliva as well. During blood-feeding, mosquitoes pierce several millimeters into the host skin and inject a cocktail of over 100 proteins, the vast majority of which have unknown functions (Ribeiro and Arcà 2009). Based on this limited understanding of both organism systems, we offer three non-mutually exclusive hypotheses to explain the observed mosquito bite-induced color change (Fig. 1):

Anesthetic: The hypothesis that a local anesthetic in mosquito saliva could cause melanophores surrounding the bite area to become increasingly visible is supported by our previous lab observation, wherein a female veiled chameleon (*Ch. calyptratus*) was injected with tricaine, an anesthetic agent (MS-222; Conroy et al. 2009). The animal's color expression changed from green to black/brown at the site of injection, followed by color change radiating out from the injection site and across the body within minutes (Fig. 2). The radial pattern is comparable to that observed from the mosquito bite, albeit at a less localized scale.

Anesthetic compounds have been identified in the saliva of the unrelated *Triatoma infestans* (Hemiptera), which inhibit sodium ion channels and prevent nerve action potentials such that the host is unaware of the blood feeding (Dan et al. 1999; Ribeiro and Arcà 2009). Similar anesthetic properties of mosquito saliva were proposed by Hudson et al. (1960). More recently, the enzyme adenosine deaminase, which acts as a numbing agent to reduce pain perception by the host, was detected in the salivary glands and saliva of *Cx. quinquefasciatus* and *Ae. aegypti*, respectively (Ribeiro and Arcà 2009). However, the presence and role of adenosine deaminase in the saliva of *Cx. quinquefasciatus* remains unclear.

Nitric oxide (NO): Another possible mechanism that may be responsible for the color change is the introduction or induction of NO during blood feeding. NO can cause darkening in teleost fishes by inducing pigment dispersion in melanophores (Hayashi and Fujii 2001; Biswas et al. 2011). A similar mechanism may cause the darkening of chameleon chromatophores.

The assassin bug *Rhodnius prolixus* is known to produce NO in its saliva, which when introduced into a mammalian host will cause vasodilation of vascular smooth muscle of the skin (Paim et al. 2017). While NO is present in the midgut of *Anopheles* mosquitoes and seems to have a role in reducing *Plasmodium* infection (Luckhart et al. 1998; Vijay et al. 2011), there are no reports of NO transfer from mosquito to host. However, *Ae. aegypti* saliva contains the vasodilator sialokinin, which stimulates host endothelial cells to produce NO, ensuring rapid blood feeding (Champagne and Ribeiro 1994; Beerntsen et al. 1999; Lefteri et al. 2022; Martin-Martin et al. 2022). Sialokinin compounds or genes are yet to be reported in *Culex* or *Ae. albopictus* but are known to be absent in *Anopheles* mosquitoes (Lefteri et al. 2022), which provides one approach for helping test this NO hypothesis.

Other Protein: Some salivary proteins aid in searching for blood vessels during biting (Ribeiro et al. 1984; Dhawan et al. 2017) while others have profound effects on the host's tissues and immune system (Vogt et al. 2018). To facilitate a rapid blood meal, some salivary proteins (such as the 16.7 kDa family unique to *Culex*) bind to serotonin and histamine in the host's blood (Ribeiro et al. 1992; Calvo et al. 2006), thus restricting the host's immune response, preventing clotting, and increasing vessel permeability (Ribeiro et al. 1992; Champagne 1994; Stark et al. 1998; O'Mahony et al. 2011; Schoenichen et al. 2019). *Anopheles* mosquitoes also have a peroxidase enzyme in their saliva, which destroys serotonin to facilitate vasodilation and easier blood feeding (Ribeiro and Nussenzveig 1993; Ribeiro et al. 1994). In mammals, the proteins can cause weals to form after feeding, however little is known about what occurs within a reptilian host during and after the blood meal.

In addition to providing intriguing hypotheses related to the mechanism(s) underlying mosquito bite-induced color change, our findings also provide interesting questions about variation in these responses across chameleon species. While we have documented observation of these color changes in free ranging *C. globifer*, *F. minor*, and *Ch. calyptratus*, as well as induced color changes in *F. lateralis* following mosquito blood-feeding events, similar observations in *F. nicosiai* and feeding trials in *F. oustaleti* failed to show these color changes (albeit note the subtle dark spots on the tail of *F. nicosiai* in Fig. 1D). While the functional basis for *F. nicosiai* and *F. oustaleti* apparently not responding with such color change is uncertain, these two species show notable difference in their skin as compared to the species that do have mosquito bite-induced color change. In particular, the skin of *C. globifer, Ch. calyptratus, F. lateralis*, and *F. minor* consists primarily of small granular scales providing a smooth and supple texture, whereas the scalation of *F. oustaleti* and *F. nicosiai* is heavily heterogeneous with numerous thick, enlarged and elevated tubercle scales providing a much more rugous texture (Glaw and Vences 2007; Tilbury 2018). The thickened nature of the skin in the latter two species may impact the penetration of any compounds inducing color change following blood feeding by mosquitos.

While determining the particular mechanism(s) of color change is outside the scope of the current study, we nonetheless serendipitously discovered multiple instances of mosquito bite-induced color change in wild chameleons. This demonstrates that citizen science can produce discoveries of previously unknown natural phenomena, as our study represents the first formal documentations of mosquitoes feeding on chameleons as well as chameleon color change induced by arthropod hematophagy. These findings provide additional insights into the parasite-host interactions, such as the mosquitoes feeding on sleeping chameleons and particularly at the mouth. In all four of the chameleon observations presented, the mosquitoes are identified as most likely belonging to the genus *Culex* (da Cunha Ramos and Brunhes 2004; Tantely et al. 2020), of which at least 50 species have been described in Madagascar (Tantely et al. 2016). This has implications for the health of endangered chameleons as well, given that certain species of *Culex* and sister genus *Uranotaenia* are known to transmit encephalitis viruses, avian malaria, and hemoparasites to reptiles (Vitek et al. 2008; Farajollahi et al. 2011; White et al. 2011; Schmid et al. 2017; Mendoza-Roldan et al. 2021). If the mosquito burden is high enough, there also exists the possibility of anemia or, rarely, fatal exsanguination (Cecco et al. 2022). Ultimately, our findings open new opportunities for future research to elucidate the behavioral and vectorial interactions of mosquitoes and their chameleon hosts, the mosquito salivary compound(s) responsible for such chromatophore change, and the chemical mechanisms that are involved.

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An Ad Hoc Assessment of Blanding's Turtle Translocation Success

Translocation, the human-mediated movement of animals between locations, is sometimes used to augment existing wildlife populations, rescue animals at risk of harm or death, and reduce human-wildlife conflict (Seddon et al. 2007; Germano et al. 2015; Sullivan et al. 2015). Unfortunately, for some taxa, the potential utility of translocation is difficult to assess because of sparse post-translocation monitoring data (Dodd and Seigel 1991; Fischer and Lindenmayer 2000). At a minimum, success requires that translocated animals remain within the area in which they are released, their survival is comparable to that of resident animals, and they reproduce successfully (Resende et al. 2020). Among reptiles and amphibians, "rescued" turtles are regularly received by wildlife rehabilitation facilities, zoos, nature centers, and wildlife managers (Pyke and Szabo 2018; Gregory et al. 2022). Without evidence for translocation success, the actions these individuals and organizations might take, other than long-term care or euthanasia, are limited. This situation is especially unfortunate for species of conservation concern that may benefit from translocation but for which opportunities for manipulative experiments to assess translocation protocols are limited.

RICHARD KING*
Northern Illinois University, DeKalb, Illinois 60115, USA
CHRIS ANCHOR
Forest Preserve District of Cook County, River Forest, Illinois 60305, USA
CINDI JABLONSKI
McHenry County Conservation District, Woodstock, Illinois 60098, USA
COLLIN JAEGER
McHenry County College, Crystal Lake, Illinois 60012, USA
DANIEL LUDWIG
Illinois Department of Natural Resources, Springfield, Illinois 62702, USA
ALBERT ROLOFF
DeKalb County Forest Preserve District, DeKalb, Illinois 60115, USA
DANIEL THOMPSON
Forest Preserve District of DuPage County, Wheaton, Illinois 60189, USA

**Corresponding author; e-mail: rbking@niu.edu*

One such species is the Blanding's Turtle, *Emydoidea blandingii*, a long-lived semi-aquatic freshwater turtle of conservation concern throughout its range (Congdon et al. 2008; USFWS 2015; COSEWIC 2016; IUCN 2021). *Emydoidea blandingii* makes long-distance overland movements that place them at risk of harm, especially in urban and agricultural landscapes (Beaudry et al. 2010). In addition, their moderate size and bright yellow throat increase their visibility and may attract the attention of people concerned for their welfare. Although their longevity and high adult survival mean that *E. blandingii* populations are likely to benefit from translocation (Paterson et al. 2021), occasional long-distance movements may result in dispersal or homing following release, potentially making translocation ineffective (Bilby and Mosby 2023).

Using data on the outcome of releases of *E. blandingii* encountered by the public in northeastern Illinois, we provide an ad hoc assessment of translocation success focused on evidence of residency, survival, and reproduction. *Emydoidea blandingii* were listed as an Illinois Threatened species in 1999