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Evolutionary Dynamics of Brown Treesnake (*Boiga irregularis*) Reproductive Ecology, with Implications for Invasive Species Control

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by

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Abstract

Invasive species represent major threats to biodiversity, global economies, and human health. Consequently, extensive research has been directed towards improving methods that restrict and contain them. Yet, control measures can also act as agents of selection by significantly impacting the reproductive capacity of invasives (in the context of “eco-evo” dynamics). The end result is that control measures subsequently alter the fitness landscape of an invasive over ecologically-relevant time, and lose their efficacy by so doing. However, adaptive management can be promoted by investigating the relationships between reproductive ecology, strength of selection, and (additive) genetic variation. In short, effective control can be developed in a management sense by unravelling those mechanisms that link reproductive ecology with selection, genetic variation, and trait heritability. In this dissertation, I considered the evolutionary consequences of these aspects with regard to the management of a quintessential invasive species, the Brown Treesnake (*Boiga irregularis*=BTS) on Guam. I used 654 single nucleotide polymorphisms (SNPs) derived from double digest restriction-site associated DNA (ddRAD) library preparation to reconstruct a 15-year multi-generational pedigree of BTS in an experimentally-closed population (N = 426). When juxtaposed with ecological data, the pedigree served to: (1) Characterize fundamental aspects of BTS reproductive ecology, (2) quantify selection on traits identified as important for mating and reproduction, (3) assess the role of selection in shaping population genetic variation, (4) ascertain the capacity of these traits to evolve in response to control, and (5) underscore the effect of trait evolution on average annual reproductive success. The results of this dissertation will promote “evolutionarily enlightened management” of invasive species in general, and invasive Brown Treesnake specifically.

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Introduction

INVASIVE SPECIES

Anthropogenic climate change (Thomas et al., 2004), habitat alteration (Travis, 2003), and invasive species (Vitousek, Mooney, Lubchenco, & Melillo, 1997) are responsible for biodiversity decline, and they do so via numerous avenues. The latter, in particular, have been deemed a major cause of species endangerment and extinction, second only to human-induced habitat loss and degradation (Simberloff, 2001), and are the number one cause of avian extinctions globally (Clavero & García-Berthou, 2005). Invasive species are known to: Disrupt community assemblies (Sanders, Gotelli, Heller, & Gordon, 2003), augment competitive exclusion, enhance niche displacement and predation (Mooney & Cleland, 2001), promote hybridization and introgression (Muhlfeld et al., 2009), and even serve as agents of natural selection (Strauss, Lau, & Carroll, 2006). Their impacts resonate not only environmentally but also sociologically, as they also facilitate major economic (Olson, 2006) and human health risks (Juliano & Lounibos, 2005).

Invasives are defined as non-native species that spread beyond their initial point of introduction, become established and abundant, and eventually result in ecological, economic, and/or human health problems (Lodge et al., 2006; reviewed in APPENDIX). They are not restricted to any particular biodiversity clade, but instead cut broadly across taxa, to include: Micro-organisms (Litchman, 2010), fungi (Dutech et al., 2012), plants (Villamagna & Murphy, 2010), insects (Facon et al., 2011), fishes (Green, Akins, Maljkovich, & Cote, 2012), amphibians (Shine, 2010), reptiles (Dorcas et al., 2012), birds (Koenig, 2003) and mammals (Donlan et al., 2007).

The mechanics of invasions span five distinct stages (Blackburn et al., 2011): (1) transport of the invasive from its native range, (2) release into the introduced range, (3) establishment, (4) spread, and (5) subsequent impacts. Myriad studies have been directed towards preventing the first three, such as identifying species with high invasive potential, predicting probable dispersal patterns (Andersen, Adams, Hope, & Powell, 2004), characterizing traits that enhance invasions (Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015), and documenting strategies that prevent establishment (Kolar & Lodge, 2002). Once an invasive is established, however, efforts quickly shift to control and eradication (Mehta, Haight, Homans, Polasky, & Venette, 2007).

REPRODUCTIVE ECOLOGY AND INVASIVE SPECIES CONTROL

Reproductive ecology [i.e., life history and ecological attributes of reproduction; reviewed in Seigel & Ford (1987)] is a key element in the establishment and persistence of an invasive. Those that exhibit high fecundity not only increase their probability of establishment but also mitigate the potential for an Allee effect and/or issues that stem from demographic and environmental stochasticity (Lockwood, Hoopes, & Marchetti, 2013). Further, the establishment of an invader hinges not only on its reproductive ecology but also with associated mechanisms that purge deleterious recessive alleles or dampen their effects. These, in turn, help explain the so-called ‘genetic paradox of invasion’ (i.e., successful despite founder effects that should depress genetic diversity and decrease the probability of establishment; Schrieber & Lachmuth, 2016).

Yet, after an initial invasion, a species also must be able to persist and cope with changes in an alien environment. Positive responses to these challenges are mediated through the mating system (e.g., selfing, monogomy, promiscuity), its characteristics (e.g., traits that promote mating and reproductive success), and associated reproductive phenomena (e.g., inbreeding, multiple paternity), as these factors influence genetic diversity and evolutionary potential (Ellegren & Galtier, 2016). In this sense, the gene pool of the founder population sets an upper limit on the amount of additive genetic variation available for selection imposed by environmental change (Prentis, Wilson, Dormontt, Richardson, & Lowe, 2008).

From a practical standpoint, an understanding of the relationships between reproductive ecology, selection by the environment, and (additive) genetic variation can promote adaptive management, in that active control alters the fitness landscape over ecologically-relevant time. This falls within the purview of ‘eco-evo’ dynamics (Rodríguez-Verdugo, Buckley, & Stapley, 2017), in that environmental change (=‘eco’) can elicit micro-evolutionary change in traits related to reproductive success (=‘evo’). This often occurs over a few short generations (Colautti & Barrett, 2013), and with subsequent impacts on population persistence. Further, phenotypic plasticity can influence the evolution of these attributes (Craig & Foote, 2001), thus augmenting evolutionary trajectories.

Eco-evo dynamics have clear implications for the management of invasive species (Dlugosch & Parker, 2008), as selection imposed by control can inadvertently modify the fitness landscape to the advantage of the invasive by actively selecting against those phenotypes that display low reproductive success. Although an understanding of these dynamics can help optimize control methods, the end result is also a moving target. Consequently, unraveling those mechanisms that link reproductive ecology with selection, genetic variation, and trait heritability in a management context is critical for the development of effective invasive species control.

THE BROWN TREESNAKE

The Brown Treesnake (*Boiga irregularis* = BTS) is a model invasive species. It is an oviparous, arboreal colubrid distributed from the Northern and Eastern coasts of Australia to Papua New Guinea and Northwest Melanesia (Rodda & Savidge, 2007). Circa 1949, 10 or fewer individuals (Richmond, Wood, Stanford, & Fisher, 2014) were introduced to the United States territory of Guam when residual World War II materials were salvaged from the island of Manus in the Admirality Archipelago (Fritts & Rodda, 1998). By 1980, it had grown to two million, with a peak density of 100 per hectare (Rodda & Savidge, 2007) that subsequently stabilized to 20-50 per hectare (Rodda et al., 2002). The success of BTS has been ascribed to a number of factors common to island invasions (APPENDIX). Among these are the presence of other established invaders that serve as trophic resources [e.g., *Hemidactylus frenatus*, *Carlia fusca*, *Rattus norvegicus* and *R*. *tanezumi* (Rodda, Fritts, McCoid, & Campbell, 1999)], an absence of predators and competitors (Fritts & Rodda, 1998), and native prey that are naïve with regard to snake predation (Cox & Lima, 2006).

BTS has caused considerable ecological damage and has been identified as the cause of catastrophic declines in Guam's avifauna (Savidge, 1987), to include 10 forest birds. Interestingly, it is the only reptile that has directly caused the extinction of another species (Mathies, Cruz, Lance, & Savidge, 2010). Three endemics are no longer found on Guam: Guam Rail (*Hypotaenidia owstoni,* extirpated), Guam Kingfisher (*Todiramphus cinnamominus cinnamominus*, extirpated), and Guam Flycatcher (*Miagra freycineti*, extinct) (Fritts & Rodda, 1998). BTS has also been implicated in the decline of other native vertebrate species (Rodda, Fritts, & Chiszar, 1997), such as the Mariana fruit bat (*Pteropus mariannus*; Wiles, 1987) and two lizards [*Perochirus ateles* and *Emoia slevini* (Rodda & Fritts, 1992)]. The endemic Guam Flying Fox (*P. tokudae*) has also been extirpated, with BTS as a contributing factor (Jones, Mickleburgh, Sechrest, & Walsh, 2009). Additionally, the decline of Guam's avifauna has had a cascading effect on community dynamics and structure (Caves, Lambers, Tewksbury, & Rogers, 2013; Mortensen, Dupont, & Olesen, 2008; Rogers, Lambers, Miller, & Tewksbury, 2012).

BTS is also detrimental to the economy (Perry & Vice, 2009) in that it predates upon domesticated chicken, requiring that eggs to be shipped to the island via air (Rodda & Savidge, 2007). Furthermore, it has damaged Guam's electrical infrastructure by shorting-out electrical wires and transformers. Power outages over a 7-year period have resulted in an annual cost >$4.5 million (Fritts, 2002), and the cost of a single outage in 1987 exceeded $250,000 (Pimentel, Lach, Zuniga, & Morrison, 2000). Impacts on (eco-)tourism, as a response to declines in native avifauna (Rodda & Savidge, 2007), represent an additional economic concern.

Additionally, BTS is of health concern to humans (Savidge, Qualls, & Rodda, 2007). Although it has a toxicity similar to that of the Copperhead, *Agkistrodon contortrix* (Rodda & Savidge, 2007), its venom is not considered dangerous to adults as it relies on capillary action as a means of transmission. Consequently, its neurotoxic and myotoxic effects (Vest, Mackessy, & Kardong, 1991; Weinstein, Chiszar, Bell, & Smith, 1991) most often provoke hospitalization only for infants (Perry & Vice, 2009).

Given the ecological and economic impacts of BTS, a variety of control methods have been implemented to reduce or eradicate its presence on Guam, but with varying degrees of success (APPENDIX). The capacity to improve BTS management by initiating studies related to reproduction has often been recognized [e.g., Engbring & Fritts (1988); Jordan & Rodda (1994); Rodda et al. (1999); Greene & Mason (2000); Moore et al. (2005); Siegel, Aldridge, Clark, Poldemann, & Gribbins (2009)]. A more thorough understanding could promote control efforts, as birth rate is a demographic parameter fundamental to population persistence (Cole, 1954). In fact, research on reproduction to improve control efforts is a component of the BTS Management Plan (Brown Tree Snake Control Committee, 1996; reviewed in APPENDIX).

Yet, studies on the reproductive ecology of BTS have been constrained by its secretive behavior (Rodda & Savidge, 2007). For example, few clutches have been found in the wild (Savidge et al., 2007), gravid females are rarely captured (Rodda et al., 1999), and mating has yet to be observed (Mathies et al., 2010). These stymie efforts to quantify mating and reproductive success and determine traits that influence fecundity. This is unfortunate in that successful control of BTS hinges on the ability to eliminate breeding individuals at a faster rate than they reproduce (Rodda et al., 2002), and to maintain efficacy of control efforts despite eco-evo dynamics. Fortunately, advances in molecular approaches [i.e., Next-Generation-Sequencing (Davey et al., 2011)] make it possible to quantify individual mating and reproductive success through genetic pedigree reconstruction (Levine et al., 2015), even in species such as BTS with cryptic behaviors and with genetic markers that are uninformative and/or limited.

PURPOSE OF RESEARCH

The overarching goal of this dissertation was to understand the influence of reproductive ecology on the evolutionary potential of BTS, and how this relationship can vary when selective regimes are imposed by control methods. In **CHAPTER 1**, I characterized the genetic mating system of an experimentally-closed population and identified traits that promote annual mating and reproductive success. In **CHAPTER 2**, I tested the manner by which selection varied across these traits, how this impacted population genetic diversity, and if selection juxtaposed with ongoing control methods. Finally, in **CHAPTER 3**, I measured the heritability of traits important to mating and reproductive success to gauge their propensity to evolve in response to control-related selection. This allowed heritability to be contextualized with regard to the continued efficacy of control measures.

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APPENDIX

An Overview of Invasive Species—

Historically, invasive species research has largely concerned itself with impacts that are far-reaching, obvious (Sakai et al., 2001), and with a wide-ranging taxonomic focus. Well-known examples include: Kudzu vine (*Pueria lobata*; Pappert, Hamrick, & Donovan, 2000), Zebra Mussel (*Dreissena polymorpha*; Astanei, Gosling, Wilson, & Powell, 2005), Africanized Honey Bee (*Apis mellifera scutellata*; (Schneider, DeGrandi-Hoffman, & Smith, 2004), Asian Grass Carp (*Ctenopharyngodon idella*; Krynak, Oldfield, Dennis, Durkalec, & Weldon, 2015), European Starling (*Sturnus vulagis*; Linz, Homan, Gaulker, Penry, & Bleier, 2007), and Norway Rat (*Rattus norvegicus*; Abdelkrim, Pascal, Calmet, & Samadi, 2005).

Invasive amphibians and reptiles (Kraus, 2009) have gathered less attention (but with several notable exceptions), and despite the fact that serious environmental impacts have resulted. These revolve around: Altering community structure and depressing native prey populations (Dorcas et al., 2012; Rodda, Fritts, & Chiszar, 1997), hybridizing with endemics (Fitzpatrick, Fordyce, Niemiller, & Reynolds, 2012; Schulte, Veith, & Hochkirch, 2012), and introducing novel diseases (Weldon, Du Preez, Hyatt, Muller, & Speare, 2004). A particularly egregious example is the Cane Toad (*Bufo marinus*) intentionally introduced to Australia as a biological control measure (Shine, 2010). Not only is it toxic to native predators (Crossland, Brown, Anstis, Shilton, & Shine, 2008; Letnic, Webb, & Shine, 2008), but also predates heavily on endemic biodiversity (Greenlees, Brown, Webb, Phillips, & Shine, 2006). Another example is the Barred Tiger Salamander (*Ambystoma tigrinum mavortium*) that hybridizes with the native and threatened California Tiger Salamander (*A. californiense*; Fitzpatrick et al., 2010). Within Reptilia, each order [save Rhynchocephalia (*Tuatara*)] contains invasive representatives [e.g., Testudines (Red-Eared Slider; Cadi & Joly, 2003), Crocodilia (Spectacled Caiman; Ellis, 1980); Squamata (Brown Anole; Eales & Thorpe, 2010)].

Invasive species within the Squamata (suborder Serpentes) have recently become a major management issue due to their top-down effects on native prey populations. For example, Burmese Python (*Python molurus*) was introduced to Everglades National Park in the 1980s (Willson, Dorcas, & Snow, 2011), and has subsequently decimated native mammalian and avian populations (Dorcas et al., 2012; Dove, Snow, Rochford, & Mazzotti, 2011). Similarly, Boa Constrictor (*Boa constrictor imperator*) was invasive to the island of Cozumel in 1971 (Martínez-Morales & Cuarón, 1999) and is implicated in the decline of native vertebrate populations, including four endemic dwarf carnivores (Cuarón, Martínez-Morales, McFadden, Valenzuela, & Gompper, 2004; Romero-Nájera, Cuarón, & González-Baca, 2007). *B. constrictor* invasions have also been reported in Aruba (Quick, Reinert, De Cuba, & Odum, 2005) and Puerto Rico (Reynolds, Puente-Rolón, Reed, & Revell, 2013).

Islands are often locations for successful snake invasions. For example (and as above), *B. constrictor* has invaded the islands of Aruba, Cozumel, and Puerto Rico (Quick et al., 2005; Reynolds et al., 2013; Romero-Nájera et al., 2007). Corn Snake (*Pantherophis guttatus*) has successfully invaded the Bahamas (Worthington-Hill, Yarnell, & Gentle, 2014), Cayman Islands (Dawson et al., 2015), as well as others (Giery, 2013). The literature is also replete with additional examples (Kraus, 2009). In fact, islands have the highest proportion of invasive species (Mooney & Cleland, 2001), exemplifying their vulnerability to introductions, and invasives are their primary cause of biodiversity loss (Courchamp, Chapuis, & Pascal, 2003). The success of invasive predators (such as snakes) has been largely attributed to several island-specific ecological considerations: The limited redundancy of native species within functional groups [i.e., ‘biotic resistance hypothesis’ (Byers & Noonburg, 2003; Elton, 1958)], simplified food webs (Byers & Noonburg, 2003; Elton, 1958), minimal community structure (Elton, 1958; Pimm, 1989), and lack of native predators and/or competitors (Fritts & Rodda, 1998; Pimm, 1989).

Brown Treesnake Control Methods—

A variety of control efforts have been implemented to reduce or eliminate BTS on Guam, and to prevent dispersal to other areas of concern [e.g., Hawai’i and other Pacific islands (Engbring & Fritts, 1988; Rodda & Savidge, 2007)] but with varying degrees of success. For example, prey items that incorporate acetaminophen pellets are placed in bait stations (Mathies, Scarpino, Levine, Clark, & Savidge, 2011) and delivered aerially (Engeman & Vice, 2001; Savarie, Mathies, & Fagerstone, 2007). Acetaminophen is effective at killing BTS (Savarie, Shivik, White, Hurley, & Clark, 2001) but the prey items are also attractive to non-target species (e.g., rats, coconut crabs) that may preemptively remove the bait (Mathies et al., 2011), thus reducing the efficacy of this approach. Furthermore, the success of bait stations depends on a variety of factors (Lardner et al., 2013).

Canine teams have also been used for BTS detection, particularly to interdict stowaways within outbound cargo (Savidge, Stanford, Reed, Haddock, & Adams, 2011), yet they have only a 35% success rate for locating free-ranging BTS (Savidge et al., 2011). Further, they have been unsuccessful in preventing individual snakes from being shipped to Hawai’i (Engbring & Fritts, 1988). Additional control efforts that require considerable time and personnel include trapping BTS with live mice (Vice & Pitzler, 2000) as well as employing nightly spotlight searches (Engeman & Vice, 2001). Further, BTS traps are biased with regard to the age class of snakes so captured (Rodda, Savidge, Tyrrell, Michelle, & Ellingson, 2007; Tyrrell et al., 2009), and also display significant but unexplained heterogeneity in trapping success (Tyrrell et al., 2009).

Positive capture techniques and successful trapping have been the subject of numerous studies, and generally fall within two categories: The success of traps, and the competence of visual searches. Regarding traps, Tyrrell et al. (2009) found that BTS trappability was positively correlated with SVL, and modestly impacted by body condition, sex, residency status, and recent capture history. Similarly, Boyarski, Savidge, & Rodda (2008) also demonstrated that trapping success was positively correlated SVL and sex (i.e., males trapped more often). However, Gragg et al. (2007) found a strong negative correlation between trappability and body condition. The effect of SVL on trapping success was additionally supported by Rodda et al. (2007), with smaller snakes evading trapping. Lardner et al. (2013) demonstrated that snakes in good body condition entered bait tubes, and that sex had no effect.

In a comparative study of trapping versus spotlight searching, Engeman & Vice (2001) found that SVL had little influence on the success of either approach. Rodda, Fritts, & Campbell (1998) estimated the number of traps and effort required to eradicate BTS from small plots and cautioned that difficulty was greatly increased by the variance in trappability among individuals. Christy, Yackel Adams, Rodda, Savidge, & Tyrrell (2010) revealed that visual searches resulted in an overall lower capture rate than did traps, yet were more effective with regard to smaller individuals, thus supporting Rodda et al. (2007). Although eradication is possible using visual searches within small plots, the effort required for island-wide eradication renders this method unfeasible (Rodda et al., 2007).

Whereas the results of visual searches are indiscriminate with respect to body size, traps reflect greater capture success, with those baited being generally more effective. However, significant unexplained heterogeneity is found among individuals with regard to trappability (Clark, Savarie, Shivik, Breck, & Dorr, 2012; Mason, Savidge, Rodda, & Yackel Adams, 2011; Rodda et al., 2002; Tyrrell et al., 2009) and represents yet another avenue for additional research. Yet it is disconcerting in that trapping is an important interdiction technique, particularly with regards to outbound cargo. Furthermore, trappability may have a heritable genetic component in BTS, as documented in fishes (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007). If so, then selection driven by trapping efforts may yield a population that is refractory to trapping (Tyrrell et al., 2009). This, in turn, would seriously hamper future control efforts.

Brown Treesnake Reproduction—

Research on BTS reproduction began in the 1980s (Savidge, Qualls, & Rodda, 2007) and has yielded insights into mating and reproductive ecology. Surprisingly, and contrary to its native range, BTS appear to breed year-round on Guam (Rodda, Fritts, McCoid, & Campbell, 1999; Rodda & Savidge, 2007), as exemplified by continuous male sperm production, and aseasonal vitellogenesis in females (Mathies, Cruz, Lance, & Savidge, 2010; Siegel, Aldridge, Clark, Poldemann, & Gribbins, 2009). Males mature at 3.1 years on Guam, while females do so at 3.7 years (per analyses of SVL and growth rate; Savidge et al., 2007). Interestingly, and again contrary to their native range, males on Guam potentially display variable reproductive tactics: Some have delayed testes development (Aldridge, Siegel, Bufalino, Wisniewski, & Jellen, 2010), whereas others will mature sexually at <50% of their maximum potential SVL, potentially providing a competitive reproductive advantage over larger males (Mathies et al., 2010). Sexual size dimorphism exists as well, but also with sex ratios skewed towards larger size class males (Savidge, 1991). Combined, these observations suggest a potential for elevated sexual selection in males, and despite the fact that male reproductive combat has only been observed in captivity (Greene & Mason, 2000).

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Chapter 1: Mating and Reproductive Success in a Highly Invasive Vertebrate Derived from Genomic Pedigree Reconstruction

ABSTRACT

The persistence of an invasive species is driven by its reproductive ecology, and a successful control program must operate on this premise. The invasive Brown Treesnake (BTS: *Boiga irregularis*) has maintained itself on Guam since being introduced circa 1949. However, its mating and reproductive ecology are enigmatic, and their contribution to its persistence has yet to be quantified. We examined these factors by reconstructing a multigenerational genomic pedigree for BTS based on 654 single nucleotide polymorphisms derived from an experimentally-closed population (N=426) established on Guam in 2004. The pedigree allowed an annual estimate of mating and reproductive success to be inferred for each individual over a 15-year period. We then employed generalized linear mixed models to gauge how well phenotypic, behavioral, and genomic data could predict sex-specific annual mating and reproductive success, with Akaike Information Criteria used to compare and rank candidate models The partial effects of age, body condition, and trappability (i.e., a propensity to enter baited traps) significantly impacted annual mating success in males (model weight = 0.73) and females (averaged model weight = 0.87), whereas annual reproductive success was significantly influenced by (a) partial effects of age, and (b) mating success, with a greater number of mating partners yielding more offspring (male and female averaged model weights = 0.92 and 0.71, respectively). Male reproductive success was also positively affected by body condition. Our results, when juxtaposed with phenotypes of trapped individuals, indicate traps may be effective in targeting fecund BTS in some regards, but not others. Work is currently underway to determine whether these traits may evolve in response to control.

INTRODUCTION

Species declines and extinctions are driven by multiple factors, the most egregious being anthropogenic climate change (Thomas et al., 2004), habitat alteration (Travis, 2003), and species introductions (Vitousek, Mooney, Lubchenco, & Melillo, 1997). The latter, in particular, have provoked negative responses in a variety of ecological contexts: Community assembly (Sanders, Gotelli, Heller, & Gordon, 2003), competitive exclusion/ niche displacement (Mooney & Cleland, 2001), interspecific hybridization/ introgression (Muhlfeld et al., 2009), and even natural selection (Strauss, Lau, & Carroll, 2006). Introductions are deemed second only to human-induced habitat loss as a major cause of species endangerment (Simberloff, 2001), yet are the primary cause of global avian extinctions (Clavero & García-Berthou, 2005). Within a more social context, invasive species also impact global economics (Olson, 2006) and human health (Juliano & Lounibos, 2005).

Species invasions are composed of five stages (Blackburn et al., 2011): Transport, release, establishment, spread, and impact. The first three have been amply researched, to include identifying species with high invasive potential, predicting their most probable dispersal routes (Andersen, Adams, Hope, & Powell, 2004), characterizing traits of successful invaders (Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015), and developing strategies to prevent establishment (Kolar & Lodge, 2002). However, once established, management efforts must then shift to control and potential eradication (Mehta, Haight, Homans, Polasky, & Venette, 2007).

The reproductive ecology of an invasive species is fundamental to its establishment and persistence, and is thus a focus of control and management. High fecundity increases the probability of establishment while reducing demographic stochasticity and/or the potential for an Allee effect (diminished fitness due to low conspecific density; Lockwood, Cassey, & Blackburn, 2013). Further, an invasive must cope with temporal changes post-invasion, and these are mediated by, and reflected in, its reproductive capacity.

The Brown Treesnake (*Boiga irregularis*=BTS), earmarked as one of the “world’s worst” invasive species (Lowe, Browne, Boudjelas, & De Poorter, 2000), was seemingly introduced circa 1949 as a single event (≤10 individuals; Richmond, Wood, Stanford, & Fisher, 2014) from the Admiralty Archipelago to the U.S. territory of Guam. Despite limited propagule pressure, its population size reached two million snakes by the 1980s (Fritts & Rodda, 1998), an increase of 40%/annum for 30+ years (Rodda & Savidge, 2007). BTS has since caused considerable ecological changes, to include extirpation/ extinction of 10 native bird species (Savidge, 1987), and population declines of endemic non-avian vertebrates (Rodda, Fritts, & Chiszar, 1997). Not surprisingly, this biodiversity decline has had a cascading effect on community dynamics and structure (Caves, Lambers, Tewksbury, & Rogers, 2013; Mortensen, Dupont, & Olesen, 2008; Rogers, Lambers, Miller, & Tewksbury, 2012). This introduction has also been detrimental to the economy (Perry & Vice, 2009) and elicits health concerns for humans (Fritts, McCoid, & Haddock, 1990).

Given these impacts, a variety of control methods have been implemented to reduce or eradicate BTS, but with varying success. Birth rate is a demographic parameter fundamental to population persistence (Cole, 1954), and thus, an in-depth understanding of reproductive ecology should be a focus for BTS control efforts. Not surprisingly, this theme has been amplified in the literature [e.g., Engbring & Fritts (1988); Jordan & Rodda (1994); Rodda, Fritts, McCoid, & Campbell (1999); Greene & Mason (2000); Moore et al. (2005); Siegel, Aldridge, Clark, Poldemann, & Gribbins (2009)]. Yet, the secretive behavior of BTS constrains field studies and stymies in-depth research on its demography (Greene & Mason, 2000; Kahl, Henke, Hall, & Britton, 2012; Mathies, Franklin, & Miller, 2004; Trembath & Fearn, 2008).

As an example, BTS mating has yet to be observed in the wild (Rodda et al., 1999), thus preventing estimates of mating success or even a characterization of its mating system (Rodda

& Savidge, 2007; Savidge et al., 2007). Gravid females are rarely captured (Moore et al., 2005; Rodda et al., 1999), and clutch size, a fundamental demographic parameter (Reed, 2005), has only been estimated by palpating several gravid females (Rodda & Savidge, 2007) and examination of ovarian follicles and oviductal eggs (Savidge et al., 2007), and with few laboratory and wild clutches examined (Aldridge, Siegel, Bufalino, Wisniewski, & Jellen, 2010; Savidge et al., 2007). Clearly, the cryptic and nocturnal life history of BTS stymies in-depth research efforts. This is unfortunate in that successful control and eradication hinges on an ability to eliminate breeding individuals more rapidly than they are replenished (Rodda et al., 2002). If phenotypes associated with elevated mating and reproductive success can be so targeted, then the potential for management to achieve this goal is enhanced considerably.

A necessary blueprint for reconstructing relationships within a population can be extrapolated from genomic DNA. Yet, genetic markers for BTS are limited, particularly with regards to fine-grained estimates of relatedness [but see Richmond et al., (2014), and Unger et al., (2015)]. However, this capacity has been expanded of late through derivation of single nucleotide polymorphisms (SNPs) that are not only cost-effective but also highly applicable to non-model organisms (Ekblom & Galindo, 2011). For pedigree reconstruction, SNP genotyping has several advantages over traditional microsatellites: A lower error rate (Smouse, 2010), broader coverage (Hauser, Baird, Hilborn, Seeb, & Seeb, 2011), and an evolution more in context with the infinite site mutation model (ISM; Morin, Luikart, & Wayne 2004).

Our central goal was to reconstruct a multi-generational genomic pedigree for BTS that would allow mating and reproduction to be inferred in the wild. To do so, we juxtaposed genome-wide SNPs identified from double-digest restriction site associated DNA (ddRAD) libraries against phenotypic and behavioral data for 426 individuals from an experimentally-closed population. Predictors of annual mating (AMS) and reproductive success (ARS) were inferred and the genetic mating system of BTS characterized. These results can be applied to assess the efficacy of existing BTS control, and to provide solid projections for adaptive management going forward.

HYPOTHESES

We hypothesized that both sexes are promiscuous (i.e., mating with more than one individual), in that this is the most common snake mating system (Serpentes; Rivas & Burghardt, 2005). We defined AMS as the number of mates with which an individual produced offspring on an annual basis, whereas ARS is the annual number of offspring produced by an individual. We hypothesized that four factors influenced AMS, with five governing ARS. Specifically, AMS and ARS are influenced by: (1) age, (2) mean body condition, (3) trappability, and (4) strength of the inbreeding coefficient. We also hypothesized that male ARS is influenced by the number of different partners with which it mates and produces offspring.

The influence of age is grounded by the fact that males and females reach sexual maturity at an estimated mean age of 3.1 and 3.7 years, respectively (Savidge et al., 2007). Second, the role of body condition stems from the reasoning that underweight individuals relative to length in either sex may lack sufficient energy reserves to search for mates (Lind & Beaupre, 2015), engage in mating and related activities [e.g., male combat (Shine et al., 2000)], and/or to produce offspring (Aubret, Bonnet, Shine, & Lourdais, 2002)].

We postulated that trappability [i.e., the propensity to enter baited traps (Le Cœur et al., 2015)] would impact both sexes in that it serves as a proxy for risk-taking behaviors (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; Wilson, Coleman, Clark, & Biederman, 1993). In this sense, positive correlations between boldness and trappability exist across taxa (Biro & Dingemanse, 2009). We predicted that individuals with high trappability would display greater values for AMS and ARS in that they would be more likely to take risks regarding mate searching and related activities. Those individuals may also enter baited traps more often due to enhanced olfactory capabilities that improve their capacity to find baited traps (Shivik, 1998; Shivik & Clark, 1997). This should also promote mating and reproductive success in that olfaction also influences mate finding (Greene, Stark, & Mason, 2001; Mathies, Levine, Engeman, & Savidge, 2013). Importantly, we recognize the complex relationship between trappability, AMS, and ARS, and thus simply offer a rationale for their association.

We also predicted that both sexes would reflect a negative relationship between AMS/ARS and inbreeding (i.e., mating between individuals that share alleles identical by descent). This would represent an echo of the founder effects manifested by BTS on Guam (Richmond et al., 2014). Finally, we hypothesized that male ARS is affected by the number of different mates with which it produces offspring. Here, sexual selection theory predicts that males with ‘cheaper’ gametes will experience increased reproductive success in response to an elevated number of matings, whereas females with ‘more expensive/ finite’ gametes will not (Bateman, 1948). Therefore, we predict that males with greater AMS will also display greater ARS, whereas females will exhibit no significant relationship between the two.

MATERIALS AND METHODS

Study Site—

The study site is a five ha enclosure on Andersen Air Force Base (northern Guam) that was fenced in 2004 to prevent immigration/ emigration of BTS (Rodda, Savidge, Tyrrell, Michelle, & Ellingson, 2007; Tyrrell et al., 2009). Tissue samples (blood, tail clips, and ventral scale clips) were collected over an eight-year span (2009–2017) from 426 unique individuals (217 females, 207 males, two of unknown sex). An algorithm was employed to extrapolate the median hatch date for each individual from sex-specific growth rates and snout-vent length (SVL) at first capture (Lardner et al., in prep).

ddRAD Library Preparation—

Genomic DNA was extracted using the QIAamp Fast DNA Tissue Kit (QIAGEN©) following manufacturer protocols. DNA concentrations were quantified with a Qubit 2.0 Fluorometer (Invitrogen, Inc.), following manufacturer protocols. High-quality genomic DNA (i.e., molecular weight >10kb) was verified by separating a 5 ul aliquot of each extract on a 2% agarose gel for 50 m at 100 mV, with visualization via GelGreen on a blue-light transluminator (Gel Doc™ EZ Imager; Bio-Rad).

We prepared extracted DNA samples using a ddRAD protocol (Peterson, Weber, Kay, Fisher, & Hoekstra, 2012) subsequently modified in Bangs, Douglas, Mussmann, & Douglas, (2018; APPENDIX). Libraries were shipped to the University of Oregon Genomic and Cell Characterization Core Facility (GC3F) for single-end sequencing (100 bp length) on an Illumina HiSeq4000. Raw Illumina sequencing reads were demultiplexed by index at University of Oregon GC3F, then downloaded to the University of Arkansas High Performance Computing Cluster (AHPCC).

Bioinformatics—

Fastq files were inspected for quality using *FastQC* (Andrews, 2014). Reads were demultiplexed by individual barcode using the *process_radtags* module of *Stacks 2.0* (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013; Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011) with default values for score limit (s=10) and sliding window size (w=0.15). The parameters used to assemble raw reads into loci were: Minimum number of identical sequencing reads to be considered a putative locus (=m), maximum number of nucleotide differences within each locus (stack) per individual (=M), and maximum number of nucleotide differences between individuals at a locus (=n; Catchen et al., 2011). Correct parameters for clustering reads into loci were identified by following published protocols (Rochette & Catchen, 2017). The correct values of these parameters were revealed by parameter optimization to be: *m*=3; *M*=2; *n*=2 (APPENDIX).

Stacks 2.0 was then used to cluster raw reads from all samples, with 75 selected for catalogue construction (Rochette & Catchen, 2017) to span the entire sampling period, include high coverage individuals, and minimize potential batch effects that could stem from digestion, ligation, and sequencing procedures. Those individuals sequenced more than once for quality control were excluded. Upon completion of the core modules (*ustacks*, *cstacks*, *sstacks*, *tsv2bam*, *gstacks*), the *populations* module identified loci present in at least 95% of individuals (*r*=0.95). To minimize linkage disequilibrium, only the first SNP at each locus was retained *(--write_single_snp*).

After removing duplicate individuals, we used *PLINK 1.9* (Purcell et al., 2007) to test for and discard loci in linkage disequilibrium (LD) and out of Hardy-Weinberg Equilibrium (HWE), and with only highly informative loci retained [=Minor Allele frequency (MAF) $\geq$0.3] to facilitate fine-scale discrimination among different relationship categories (Anderson & Garza, 2006; Huisman, 2017). For LD and HWE tests, all individuals (n=24) born from 2002–2004 (=year of fence construction) were considered as founders. We tested for LD with the *--indep* function, evaluating 50 SNP windows, five SNPs at a time and with a variance inflation factor (VIF) cut-off=2.

Pedigree Reconstruction—

The *R* package *Sequoia* (Huisman, 2017) employed SNP genotypes, sex, and birth year to iteratively reconstruct a maximum-likelihood multigenerational pedigree, while minimizing erroneous assignments. Initial parentage assignments were accomplished with the genotype file and a life history file with *MaxSibiter*=0. This allowed the initial pedigree scaffold to be scanned for obvious errors, as well as for duplicates accidentally retained. The parameter data frame (*Specs*) was altered to increase *MaxSibshipSize*=100, *MaxSibiter*=40, and *UseAge*='Extra,' per recommendations (J. Huisman, *personal communication*, 9 April 2018). All other parameters remained at default. The full pedigree was constructed by setting the altered parameter file as the *SeqList* read, with the accuracy of the pedigree assessed (APPENDIX). *Sequoia* was run using *R v. 3.4.3* (R Core Team, 2013). It was subsequently visualized using the *R* package *Pedantics* (Morrissey & Wilson, 2010; FIGURE 1) in *RStudio* (*R v. 3.5.0*; RStudio Team, 2015), with AMS and ARS calculated for each individual.

Statistical Analyses—

We fit generalized linear mixed models (GLMMs) using the *R* package *glmmTMB* (Brooks et al., 2017) to test the effects of predictor variables on sex-specific AMS and ARS, with each sex (males=207; females=217) modelled separately. Two individuals of unknown sex were excluded. All statistical analyses were conducted in *RStudio* (*R v. 3.5.0*; RStudio Team, 2015).

Prior to model fitting, we employed plots to visualize the structure and distribution of our data. The potential presence of interactions among explanatory variables was gauged by generating co-plots, with collinearity tested among explanatory variables for AMS and ARS (Zuur, Ieno, & Elphick, 2010). To do so, we visually inspected correlation matrices and calculated VIFs with the *R* package *MCtest* (Imdadullah, Aslam, & Altaf, 2016), with no evidence of significant collinearity among variables [all VIFs<2 (Zuur, Ieno, & Elphick, 2010)].

We did not model interactions among explanatory variables in sex-specific GLMMs of AMS and ARS for several reasons. First, we had no *a priori* expectation that explanatory variables would interact to influence AMS or ARS (Harrison et al., 2018). Second, visualization of potential interactions with co-plots did not indicate strong interactions among predictor variables (Bolker et al., 2009; Zuur & Ieno, 2016; Zuur et al., 2010). Third, we avoided over-parameterization of our models by eliminating interaction terms (Harrison et al., 2018).

We used a Poisson error distribution with a log-link for all GLMM analyses, chosen because of its appropriateness for count data, with AMS and ARS >0 (Zuur, Ieno, Walker, Savaliev, & Smith, 2009), and means of our response variables <5 (DuVal, 2012). Choice of this distribution was validated by testing for over-dispersion (all $p>0.05$), and by plotting scaled residuals against predicted values [(simulated with the *DHARMa R* package (Hartig, 2017)].

We modelled sex-specific AMS as a linear function of four fixed and two random effects. Fixed annual effects included mean body condition index (BCI), age, trappability, and the genomic inbreeding coefficient [F_{hat3} (Yang, Lee, Goddard, & Visscher, 2011)]. Random effects included individual and year (Bolker et al., 2009). Multiple repeated measurements were accounted for with the “individual” term so as to avoid pseudo-replication, whereas year was included to accommodate temporal variation (e.g., different levels of sampling effort or different numbers of traps deployed per year).

Annual mean BCIs were estimated by taking the residuals of the regression of log-transformed annual mean body mass versus log-transformed annual mean SVL (Schulte-Hostedde, Zinner, Mllar, & Hickling, 2005). Annual trappability was assessed by summing the number of times an individual was trapped in a given year [see Réale et al. (2000), Le Cœur et al. (2015)]. Age was appraised by subtracting estimated birth year from the year under consideration. Finally, a genomic measure of inbreeding [F_{hat3} (Yang et al., 2011)] was derived for each individual using *PLINK 1.9*.

Similarly, we modelled sex-specific ARS as linear functions of fixed and random effects. Fixed effects included mean BCI, age, trappability, genomic inbreeding coefficient, and number of mates with which the individual produced offspring (=AMS). We also included individual and year as random effects in our GLMMs of ARS (Bolker et al., 2009).

We used the *dredge* function of the *R* package *MuMIn* (Barton, 2016) to fit all candidate models and to rank them using Akaike Information Criterion (Akaike, 1973), as corrected for small sample size (=AICc; APPENDIX TABLES S2–S5). Model averaging (Burnham & Anderson, 2004) was employed to identify the components of the average model when top ranked models could not be distinguished from one another (i.e., delta<2; APPENDIX TABLES S2–S5)). Ninety-five percent confidence intervals (CIs) were calculated for each parameter estimate as ± 1.96 x the unconditional standard error (SE), with significance of parameter estimates determined by the overlap of their 95% CIs with zero and the relative importance (RE) of parameters in averaged models (Grueber, Nakagawa, Laws, & Jamieson, 2011).

RESULTS

ddRAD Sequencing and Bioinformatic Processing—

Ilumina sequencing of ddRAD libraries resulted in 1,590,917,152 raw reads, with mean number of raw reads/individual=3,734,547 (standard deviation (SD) = ±1,114,685.18). When considering samples duplicated for quality control, sequencing resulted in 1,971,406,088 raw reads (μ=3,650,752 reads ±1,105,292.25). Mean sequencing coverage/individual=25.97x (±8.26), while mean coverage/sample=24.80x (±8.32), including duplicates.

Once raw reads were clustered into SNP loci, filtering with the *populations* module of *Stacks 2.0* resulted in 6,180 SNPs, each present in at least 95% of sequenced BTS (N=426). Of the 6,180 SNPs that passed filtering, 217 were discarded due to departures from HWE ($p<0.05$), 482 with LD (VIF>2), and 4,827 that had allele frequencies <MAF threshold (=≤0.3). All remaining loci (n=654) were used for pedigree reconstruction.

Pedigree Reconstruction—

Sixty-nine known females were assigned as dams of 199 individuals (Appendix Figure S2), while 51 known males as sires of 257 individuals (Appendix Figure S3). The pedigree had a maximum depth of three generations (i.e., individuals linked directly with parents and grandparents), but the entire pedigree spanned 15 years and included individuals with estimated birth years from 2002 to 2016 (Figure 1).

AMS was low in any given year for both sexes. Mean male AMS=0.24 (±0.96) mates/year, while that for females=0.16 (±0.49). ARS was also low for each, with mean male

ARS=0.35 (±1.66) offspring/year while mean female ARS=0.24 (±0.80). However, when only reproducing individuals were considered, a promiscuous mating system was evident in that both sexes produced offspring via multiple mates each year. Males averaged 2.25 females/year (±2.05; APPENDIX FIGURE S4), whereas females produced offspring with an average of 1.34 males/year (±0.64; APPENDIX FIGURE S5). Of individuals that reproduced, mean male ARS=3.34 (±4.01; APPENDIX FIGURE S6) offspring/year while mean female ARS=2.01 (±1.33; APPENDIX FIGURE S7). Thirteen individuals were assigned as parents of 15 offspring for which the other parent of the offspring could not be assigned to a known or dummy parent by *Sequoia*. The births of these 15 offspring were excluded from estimation of AMS and ARS for downstream analyses so as to avoid overestimation of mating success. Preliminary analyses (i.e., GLMMs including these births in estimates of AMS and ARS) demonstrated that their exclusion from further analyses had no effect on the significance of results (not shown).

GLMMs of AMS and ARS—

We analyzed 1,396 complete records of annual mating success, annual reproductive success, phenotypic and behavioral data for 424 individuals over 15 years that included 661 records for males and 735 for females. Records from 2014 were excluded from analyses, as phenotypic and behavioral data were not collected from individuals that produced offspring during this year. Mean age of reproduction was 3.69 (±1.08) and 3.94 (±1.20) years for males and females, respectively. On average, annual male BCI=-0.02 (±0.19) while female BCI=0.02 (±0.09). Further, males were trapped on average 1.34 (±2.96) times/year, while for females it was 1.47 (±3.49). The mean level of genomic inbreeding for females=0.03 (±0.09), with 71% (N=154) having positive F_{hat3} values, while 8.3% (N=18) had values >0.125 [approximating half-sib mating (Huisman, Kruuk, Ellis, Clutton-Brock, & Pemberton, 2016)]. The mean level of genomic inbreeding for males=0.02 (±0.12), with 14 (6.8%) having F_{hat3} values >0.125, while 137 (66.2%) had positive F_{hat3} values.

The top model for male AMS (weight=0.73) included age, BCI, and trappability as fixed effects (APPENDIX TABLE S2). Two averaged models of female AMS (cumulative weight=0.87) included age, BCI, trappability, and level of inbreeding as fixed effects (Appendix Table S3). Ninety-five percent CIs of parameter estimates that did not overlap with zero indicated significant positive partial effects of age, BCI, and trappability on AMS for both sexes (TABLE 1). The significance of these parameters is further supported by their RIs, which were each equal to 1.0.

Four averaged models of male ARS (cumulative weight=0.92; APPENDIX TABLE S4) and four of female ARS (cumulative weight=0.71; APPENDIX TABLE S5) included age, trappability, inbreeding, and AMS as fixed effects, with male models including BCI as a fixed effect as well. Significant partial effects of AMS and age on ARS were found in both sexes such that each produced more offspring during those years in which they were older and/or mated with more partners (Table 2). Males with greater BCIs also had significantly greater ARS than did males with lower BCIs, but females lacked such an effect.

DISCUSSION

Characterization of the Mating System—

Our hypothesis of a promiscuous mating system for BTS was supported, in that both sexes produced offspring with multiple mates each year. Promiscuity is the most common type of mating system in snakes (Rivas & Burghardt, 2005), although polygyny (multiple mating only in males) and polyandry (multiple mating only in females) are also prevalent (Duvall, Schuett, & Arnold, 1993; Kissner, Weatherhead, & Gibbs, 2005).

Predictors of AMS—

We hypothesized that AMS in both sexes would be influenced by age, BCI, trappability, and degree of inbreeding, and our data supported the first three factors. Older individuals, those in better body condition, and those frequenting baited traps also mated with more partners. Literature supports the argument that older individuals experience greater annual mating success when compared to younger individuals across taxa [e.g., Red Deer (Nussey et al., 2009), Spotted Sandpipers (Oring, Reed, Colwell, Lank, & Maxson, 1991)].

We also predicted that BCI would influence annual mating success. In this sense, individuals with better body condition have greater energy reserves that supported a variety of mating-related behaviors. For example, larger males gain access to females by being successful in confrontations with smaller males (Greene & Mason, 2000). Larger females, on the other hand, reflect adequate energy reserves for production of offspring (Aubret et al., 2002) and, given this, may receive elevated attention from males. Sufficient energy reserves would also permit mate searching in both sexes (Lind & Beaupre, 2015). Furthermore, a better body condition may allow more time for mate searching in that competing activities such as foraging are less mandatory (Beaupré, 2008).

We also predicted that trappability would influence mating success in both sexes. Trappability has often been used as a proxy for propensity of individuals to engage in risk-taking behaviors (Biro & Dingemanse, 2009). Presumably, individuals bold enough to enter baited traps will also take risks to acquire mates. For instance, movement by bold individuals in search for mates may increase their risk of predation, while those less bold would not, with the likelihood of encountering potential mates subsequently diminished (Sih, Bell, & Johnson, 2004). Trappability may also correlate with the ability of an individual to detect chemical stimuli from baited traps. Those with better olfactory capacity will enter traps more often (Shivik, 1998). BTS also utilize chemical stimuli (i.e., pheromones) to find mates (Greene et al., 2001), so it is likely that individuals with better chemosensory abilities will not only find baited traps more frequently but also have greater success in finding mates.

We failed to reject the hypothesis that inbreeding has an effect on sex-specific AMS. This result was somewhat surprising because the majority of individuals in our study population had inbreeding values (F_{hat3})>0, with several (~8% females; ~7% males) with half-sib parental relationships (F_{hat3} >0.125). Mating success in the wild is negatively impacted by the degree to which focal individuals are inbred (Janicke, Vellnow, Lamy, Chapuis, & David, 2014; Joron & Brakefield, 2003), and thus a lack of association is puzzling.

Although we found no significant direct partial effect, inbreeding may instead manifest itself indirectly by influencing other traits that, in turn, impact AMS. For example, inbreeding is correlated with an increase in risk-taking behavior, such that inbred individuals are bolder and assume greater risks than those not inbred (Richardson & Smiseth, 2017). In addition, inbreeding depression may impact other fitness traits like overall longevity, such that a motivation to mate may be a life-history response that counters a shortened lifespan (De Boer, Eens, & Müller, 2018). The effects of inbreeding may also be context-dependent, with negative impacts more pronounced under stressful conditions (Armbruster & Reed, 2005). However, Guam has a relatively constant environment (Rodda et al., 1999) that may counter environmental stress and act to dampen negative effects of inbreeding on AMS. Further, individuals may avoid inbreeding effects through behavioral plasticity (Lucia-Simmons & Keane, 2015). Finally, inbreeding may simply exert minimal effects on AMS (Gooley, Hogg, Belov, & Grueber, 2017). An investigation to determine why this population has high levels of inbreeding yet no evidence of inbreeding depression on AMS provides additional avenues for research.

Predictors of ARS—

We hypothesized that male ARS would be affected by AMS, age, BCI, trappability, and degree of inbreeding, but found only the first three as significant. On the other hand, we predicted female ARS would only be affected by age, inbreeding, BCI, and trappability, yet only found significant influences with regard to the age and AMS.

We were surprised by two of these results. First, we hypothesized that male ARS, but not female, would be affected by AMS. Yet, both sexes experienced a significant increase as number of mating partners increased. This is contrary to sexual selection theory, in that males should experience elevated fitness as numbers of mating partners increase, whereas females should experience no such gain (Arnold & Duvall, 1994). Empirical studies across taxa support this pattern (Janicke, Häderer, Lajeunesse, & Anthes, 2016).

However, our results indicated that sexual selection acts on both sexes such that an increase in ARS reflects an increase in AMS. Our predictors for AMS indicated several factors influential in both sexes (i.e., age, BCI, trappability), thus highlighting several avenues by which selection on phenotypes may influence competition for mates, and ultimately, reproductive success. For example, a trait like BCI may be subjected to female sexual selection in that a greater BCI may appear ‘sexier’ to males, perhaps through female hormonal activity (Aubret et al., 2002). Indeed, recent work has emphasized the importance of sexual selection in females (Collet, Dean, Worley, Richardson, & Pizzari, 2014). It may also be context-dependent for females to experience an increase in ARS with an increase in AMS [e.g., related to the operational sex ratio (Jones, Arguello, & Arnold, 2004)], and consequently the prevalence of temporal variation in AMS is a topic of ongoing BTS research.

Additionally, only male ARS was significantly affected by BCI. Although the energetic status of males often influences their ability to mate [e.g., Red-Sided Garter Snake (Richard Shine & Mason, 2005), Timber Rattlesnake (Lind & Beaupre, 2015)], the relationship between BCI and male reproductive success in snakes remains somewhat nebulous (Shine & Mason, 2005). Males seemingly contribute little energy to actual reproductive success, in that gamete production requires limited energy (Aubret et al., 2002). However, they do expend considerable energy in related activities (Lind & Beaupre, 2015; Shine & Mason, 2005). It is possible that the significant effect of BCI on ARS is due to mate acquisition, or even the physical ability of males to mate [e.g., adequate plasma testosterone levels (Bonnet & Naulleau, 1996), elevated corticosterone levels due to food stress (Waye & Mason, 2008)]. Indeed, chronic stress and elevated corticosterone levels are associated with low BCI (Waye & Mason, 2008), whereas elevated male BCIs are related to higher levels of plasma testosterone (Mathies, Cruz, Lance, & Savidge, 2010). In addition, elevated corticosterone and reduced plasma testosterone negatively affect reproduction in male BTS (Aldridge et al., 2010; Moore et al., 2005). Yet, male BCI may also have the capacity to directly influence reproductive success. Male body size is associated with testes mass, such that large male BTS may in fact have greater rates of sperm production, and an increased capacity to fertilize females (Mathies et al., 2010).

We were also surprised that females did not experience an increase in ARS coincident with an increase in BCI. However, mean annual female BCI was positive (μ=0.02±0.09). Therefore, the majority of females may have had BCI at or above a threshold necessary for annual reproduction (Naulleau & Bonnet, 1996). Considering that we found an effect of BCI on female mating success, it is also possible that its effects on ARS are instead expressed through female AMS. Further, females may actively forage while vitellogenic, so as to acquire adequate energy for reproduction [i.e., income breeding (Bonnet, Bradshaw, & Shine, 1998; Waye & Mason, 2008)]. Future work will be required to determine why males, but not females, have higher ARS with better BCIs.

Implications for Control—

A variety of control efforts have been implemented to reduce or eliminate BTS on Guam, and to prevent its dispersal to other areas (Engbring & Fritts, 1988; Rodda & Savidge, 2007). Baited traps are a primary method and improving trap success will likewise promote BTS management. Here, we interpreted our results in the context of common phenotypes of trapped individuals.

First, several studies have explored the relationship between size and trappability [e.g., Rodda et al. (2007), Boyarski, Savidge, & Rodda (2008), Tyrrell et al. (2009), Lardner et al. (2013)], with larger individuals trapped more frequently than those smaller [but see Engeman & Vice (2001)]. SVL increases with age but the latter was chosen in this study as a predictor for AMS and ARS so as to avoid collinearity with body condition. Thus, traps seem effective at capturing individuals with greater AMS and ARS because individuals with larger SVLs (=older) are predominantly taken.

While several studies have focused on the relationship between trapping success and BCI, their results were variable. For example, Tyrrell et al. (2009) and Lardner et al. (2013) found a positive correlation between BCI and the accession of traps and bait tubes, respectively, whereas Gragg et al. (2007) and Boyarski et al. (2008) found a negative correlation. Our study demonstrated that BCI has a positive effect on AMS, with the latter having a positive effect on ARS for both sexes. We also identified a significant direct effect of BCI on male ARS. Given the relationship between BCI and AMS/ARS, its uncertain effect on trapping success is of concern. In this sense, individuals exhibiting larger or smaller values of AMS and ARS could be removed by traps. A topic for future work must determine if trapping removes fecund individuals, particularly with regard to factors contributing to BCI (e.g., metabolic rate, chemosensory ability used to find food) as heritable traits.

Finally, it is promising that overall trappability is related to AMS in both sexes. We found individuals with higher trappability also acquired more mates and consequently left more offspring. Therefore, targeted individuals may be those with higher AMS and ARS, and their removal can potentially depress the birth rate of the population. However, previous studies have identified significant unexplained heterogeneity in trappability among individuals (Clark, Savarie, Shivik, Breck, & Dorr, 2012; Mason, Savidge, Rodda, & Yackel Adams, 2011; Rodda et al., 2002; Tyrrell et al., 2009). This is disconcerting in that trapping is an important interdiction technique, particularly for capture of snakes in outbound cargo (Engeman & Linnell, 1998). Even more concerning is that trappability may have a heritable genetic component, as documented in fishes (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007). If the trappability of a snake is in fact heritable, selection may then yield a population with overall lower AMS and ARS, but one that is also trap-shy (Rodda et al., 2002; Tyrrell et al., 2009). We are currently evaluating the heritability of being trap-prone to ascertain whether the population might evolve to become less trappable. We are likewise assessing the effects of artificial selection on trappable phenotypes, and how this may impact AMS and ARS.

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APPENDIX

Figures and Tables—

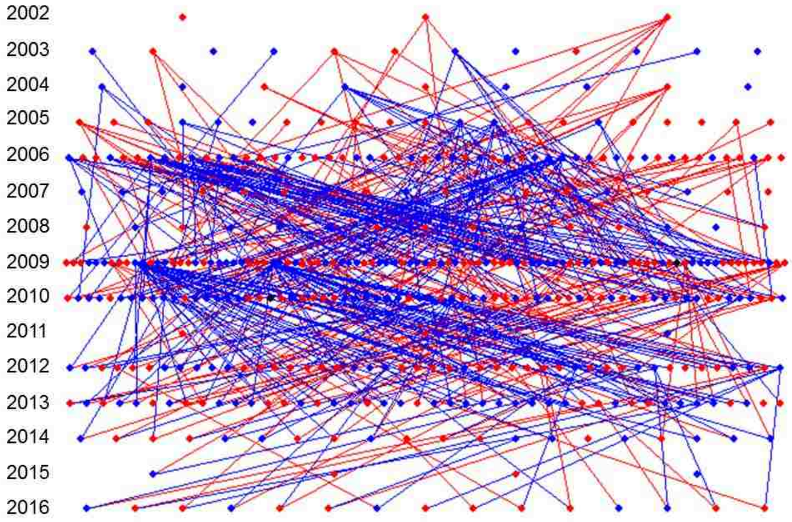

FIGURE 1. A multigenerational pedigree of an experimentally-closed population of Brown Treesnake (*Boiga irregularis*) reconstructed from 654 SNPs (single nucleotide polymorphisms) with high minor allele frequencies ($\geq$0.3). Vertical axis=pedigree years. Blue dots represent male births (N=207), with blue lines linking them to offspring. Red dots represent female births (N=217), with red lines linking them to offspring. Black dots represent births of individuals with unknown sex (N=2).

TABLE 1. (Model-averaged) results for generalized linear mixed models (GLMMs) of annual mating success (AMS) for male (N=207) and female (N=217) Brown Treesnake (*Boiga irregularis*) from an experimentally-closed population on Guam. AMSs were modelled as linear functions of four annual fixed effects (=Parameters): Age, trappability, body condition index, and the individual's level of genomic inbreeding (='Inbreeding'). GLMMs also included individual and year of sampling as random effects (not shown). All GLMMs employed a Poisson error distribution with a log-link. Estimate=statistical value; SE=standard error; 95% CI=5% and 95% confidence limits; RI=relative importance of parameter after model averaging.

Parameter		Estimate	SE	95% CI	RI
Males:					
	Intercept	-5.78	0.83	-7.41, -4.15	-
	Age	0.50	0.12	0.26, 0.74	-
	Trappability	0.13	0.04	0.05, 0.21	-
	Body Condition	5.48	1.00	3.52, 7.44	-
Females:					
	Intercept	-5.63	0.88	-7.35, -3.91	-
	Age	0.50	0.09	0.32, 0.68	1.00
	Trappability	0.06	0.02	0.02, 0.10	1.00
	Body Condition	2.62	0.78	1.09, 4.15	1.00
	Inbreeding	-0.27	0.84	-1.92, 1.38	0.31

TABLE 2. Model-averaged results for generalized linear mixed models (GLMMs) of annual reproductive success (ARS) for male and female Brown Treesnake (*Boiga irregularis*) from an experimentally-closed population on Guam. Male (N=207) and female (N=217) ARS were modelled as linear functions of five fixed effects (='Parameter'): Age, trappability, body condition index (='BCI'), level of genomic inbreeding (='Inbreeding'), and the number of partners with which the individual produced offspring (='Number of Mates'). GLMMs included individual and year of sampling as random effects (not shown). Male and female GLMMs used a Poisson error distribution with a log-link. Estimate=statistical value; SE=standard error; 95% CI=5% and 95% confidence limits; RI=relative importance of parameter after model averaging

Parameter		Estimate	SE	95% CI	RI
Males:					
	Intercept	-4.75	0.55	-5.83, -3.67	-
	Age	0.38	0.10	0.18, 0.58	1.00
	Trappability	0.03	0.04	-0.05, 0.11	0.51
	Body Condition	2.47	0.93	0.65, 4.29	1.00
	Inbreeding	-0.28	0.74	-1.73, 1.17	0.33
	Mating Success	0.93	0.10	0.73, 1.13	1.00
Females:					
	Intercept	-5.05	0.68	-6.38, -3.72	-
	Age	0.30	0.10	0.10, 0.50	1.00
	Trappability	0.02	0.03	-0.04, 0.08	0.50
	Inbreeding	-1.28	1.54	-4.30, 1.74	0.56
	Mating Success	1.79	0.19	1.42, 2.16	1.00

ddRAD Library Preparation—

Briefly, 1,000–2,000 ng of genomic DNA per individual were digested in a 30 ul reaction with 1 ul each of restriction enzymes *Msp1* and *Pst1*, 5 ul 10x CutSmart® Buffer (New England BioLabs® Incorporated), and 23 ul HPLC grade water. Samples were incubated during digestion for 24 h at 37 °C in a Veriti 96-Well Thermal Cycler (Applied Biosystems™). Successful digestion was confirmed by separating 5 ul of each digest on a fresh 2% agarose gel, with visualization using GelGreen on a blue-light transluminator.

Digests were cleaned with Agencourt AMPure XP beads (Beckman Coulter, Inc.) and ligated with a P1 adaptor with a unique five base pair (bp) barcode. A total of 48 unique barcodes allowed for subsequent pooling and sequencing of DNA in sets of 48 individuals (=one ddRAD library). Digested DNA concentrations were standardized among samples within libraries to promote equal coverage. Ligation was performed in a 30 ul reaction/individual, consisting of 22 ul digested sample, 2 ul P1 adaptor, 3 ul 10x T4 DNA ligase reaction buffer (New England BioLabs® Inc.), 2 ul P2 adaptor, and 1 ul T4 DNA ligase (New England BioLabs® Inc.). Ligation occurred in a Veriti 96-Well Thermal Cycler using a temperature profile of 22 °C/60 minutes, 65 °C/10 minutes, a decline of 1% ramp rate at ~1 °C per minute, and a 20 °C hold. Ligated samples were pooled in sets of 48, followed by an additional AMPure XP cleanup.

We used a Pippin Prep (Sage Science) to perform size-selection of ligated, pooled samples. An appropriate fragment size range was identified for parentage and kinship analyses by performing an *in silico* digest with *FRAGMATIC* (Chafin, Martin, Mussmann, Douglas, & Douglas, 2017). Simulated numbers of fragments were then compared with results from previous *in vitro* preparation of test libraries (see below) to identify an optimal size selection (=262-350 bp).

Finally, Phusion® PCR was performed on each size-selected library. This was accomplished using four 20 ul reactions per library [=5 ul size-selected DNA, 5.8 ul HPLC grade water, 4.0 ul Phusion® HF buffer (New England BioLabs® Inc.), 0.5 ul $MgCl_2$ (50 mM), 0.5 ul dNTP (10 mM), 2.0 ul PCR 1 primer (2 uM), 2 ul PCR 2 indexed primer (2 uM), and 0.2 ul Phusion® high-fidelity DNA polymerase (New England BioLabs® Inc.]. Temperature profile for Phusion® PCR in a Veriti Thermal Cycler was: 1 cycle of 98 °C/1 minute; 12 cycles of 98 °C/15 s, 62 °C/30 s, 72 °C/30 s; 1 cycle of 98 °C/7 m; and a 20 °C hold. Importantly, sets of libraries sequenced in the same lane were ligated with different indices, allowing for 96 individuals to be sequenced/lane (=2 indices, 48 barcodes). Phusion® PCR was followed by a final AMPure XP cleanup, with DNA concentrations quantified using a Qubit 2.0 Fluorometer. To minimize batch and lane effects, DNA samples were semi-randomly grouped into different digestions, ligations, and sequencing runs. Additionally, to confirm batch effects did not influence our sequencing results, 114 individuals were sequenced twice, following separate ddRAD library preparations.

Optimization of ddRAD Size Selection—

At the time of *in silico* analyses (November, 2014), only three snake draft genomes were available for this study: Burmese Python (*Python bivittatus*; Castoe et al., 2011), King Cobra (*Ophiophagus hannah*; Vonk et al., 2013), and Speckled Rattlesnake (*Crotalus mitchelli*; Gilbert et al., 2014). King Cobra resides within the same superfamily (Colubroidea) as BTS and presumably shares a more recent common ancestor. However, the King Cobra genome consisted of unassembled contigs at the time of our *in silico* digests and may have resulted in inaccurate estimates of fragment size frequencies [although some have argued that unassembled contigs have the potential to allow for unbiased *in silico* estimates (see Lepais & Weir (2014)].

To avoid potential biases, the Burmese Python genome was instead chosen. Although within a different superfamily (Henophidia) than BTS [divergence time between clade containing Pythonidae and Colubridae is approximately 50 million years (Castoe et al., 2011)], its draft genome at the time of *in silico* simulations represented a scaffold and was thus more appropriate for ddRAD cut-site simulation. The Burmese Python haploid genome is 1.44

gigabases (gb) in size with an estimated GC content of 39.7% (Castoe et al., 2011). Although no genome size estimates exist for BTS, another species within the genus, Blanding's Treesnake (*B. blandingii*), has a genome size estimated as 1.86 gb. The size in base pairs of the Blanding's Treesnake haploid genome was calculated by converting the diploid genome in picograms (De Smet, 1981) to gigabases, then dividing this value (= 3.7 gb) by two. Additionally, the GC content of the Blanding's Treesnake genome was estimated as 51.5% by multiplying the GC content of the Burmese Python genome by the size of the Blanding's Treesnake haploid genome, then dividing this value by the size of the Burmese Python haploid genome. GC content (= guanine-cytosine content) is a measure of the nucleotide composition of the genome (Šmarda et al., 2014) and can impact NGS base-calling and coverage (Benjamini & Speed, 2012).

The *in silico* genome digestion was conducted using program *FRAGMATIC* (Chafin et al., 2017) which simulates the digestion of genomes by two user-specified restriction enzymes. The selected restriction enzymes were *PstI* (*Providencia stuartii* gene in *E. coli;* cut site recognition sequence = CTGCA^G) and *MspI* (*Moraxelle spp.* gene in *E. coli*; cut site recognition sequence = C^CGG). The simulation was conducted on the Arkansas High Performance Computing Cluster (AHPCC). First, the Burmese Python draft genome was downloaded from the National Center for Biotechnology Information (NCBI) and uploaded to AHPCC. The whole genome scaffold was then split into individual, numerically ordered FASTA files that served as input to *FRAGMATIC*. Output included a frequency distribution plot and a listing of ddRAD fragments within different size classes.

During *in silico* digestion and ddRAD planning (November, 2014), the phylogenetic history of the BTS invasion was inferred using mitochondrial and nuclear markers (Richmond, Wood, Stanford, & Fisher, 2014). Consequently, estimates of nucleotide diversity in Guam became available. Across four nuclear loci (i.e., RAG-1, MyHC-2, *Bi*TBP, *Cmos*), nucleotide diversity within Guam individuals ranged from 0.0004 (*Cmos*) to 0.0030 (RAG-1) with the number of alleles per locus ranging from two (RAG-1) to four (*Bi*TBP).

A comparison of the length of these loci (i.e., RAG-1: 1054 bases; MyHC-2: 561 bases; *Bi*TBP: 1014 bases; *Cmos*: 954 bases) with their respective numbers of alleles allowed for predictions regarding the frequency of SNPs that could be expected in individuals from the study population. Considering that only ddRAD fragments ranging in lengths of approximately 200–550 bp can be selected due to the limitations of Illumina platform sequencing (Davey & Blaxter, 2010), the predicted frequency is approximately one SNP per four ddRAD fragments sequenced. However, a more conservative estimate is a frequency of one SNP for every 10 loci, given that the population experienced a genetic bottleneck associated with the founder event in the late 1940s (Richmond et al., 2014).

Previous studies have shown parentage and kinship in a wild population can reliably be inferred with as few as 50–60 SNPs and yield resolution comparable to that of 20 polymorphic microsatellite loci (e.g., Anderson & Garza, 2006; Tokarska et al., 2009; Santure et al., 2010; Smouse, 2010; Rasic, Filipovic, Weeks, & Hoffmann, 2014). However, the bi-allelic nature of SNP markers, their low genotyping error rate, and the relative ease with which thousands can by identified through ddRAD sequencing, allows many more SNPs to be produced than the minimum number required for parentage and kinship assignment (i.e., Tokarska et al., 2009; Santure et al., 2010; Senn et al., 2013; Rasic et al., 2014). The inclusion of many more SNPs has particular importance for assignment of parentage and kinship, as the Guam population was founded by very few individuals [i.e., 1–10 snakes (Richmond et al., 2014)]. It is therefore likely that the minimal number of SNPs employed in other studies may be insufficient for resolving relationships in our study population [but see Tokarska et al. (2009)]. Therefore, we established a target of 2,000 polymorphic SNPs. Similar numbers have been employed in recent studies of parentage and kinship in other organisms [e.g., Mosquitos (Rasic et al., 2014); European Bison (Tokarska et al., 2009); Eurasian Beaver (Senn et al., 2013); Pigs (Lopes et al., 2013)].

A conservative estimate of one SNP per 10 ddRAD loci would thus require 20,000 ddRAD loci in this study. However, quality filtering and uneven coverage across the genome generally eliminate approximately 50% of sequenced loci. Thus, twice as many loci were targeted, yielding approximately 40,000 ddRAD loci at 20-25x coverage.

Such an estimate is of importance in ddRAD fragment size selection. For example, several fragment size classes were arbitrarily selected with regards to their frequencies in the *in silico* digestion of the Burmese Python genome, allowing for an extrapolation to the BTS genome. This was achieved by multiplying the size of the Blanding's Treesnake haploid genome (closest relative to BTS for which genome size has been estimated; = 1.86 gb) by the fragment frequency in the Burmese Python haploid genome, and then by dividing this value by the size of the Burmese Python haploid genome (= 1.44 gb; Castoe et al., 2011). From these calculations, it was determined that a variety of 75–100 bp size classes ranging from 250 to 350 ±50 bp would yield a sufficient number of fragments to accrue approximately 2,000 SNPs. An examination of the frequency of all fragment sizes in the Burmese Python genome provided confidence that the preferred size classes did not contain repeat elements [i.e., genome features that complicate the detection of SNPs and monopolize sequencing effort (Leggett & MacLean, 2014)].

Two BTS ddRAD libraries were prepared to test effects of different size selection ranges on locus recovery (=same fragments across all individuals) and coverage depth (=number of times each locus is sequenced). The first library included 24 randomly selected blood samples and tested a broader size range of fragments (i.e., more fragments; size range spanning 100 bp). The second library was from 48 randomly selected blood samples and evaluated a more restricted size range (i.e., fewer fragments; size range spanning 75 bp). For comparative purposes, 10 individuals were included in both libraries (=replicate samples). Therefore, a total of 54 unique samples were evaluated in an effort to optimize size selection. The two libraries were single-end sequenced on an Illumina HiSeq4000 (Illumina, Inc.). The smaller size-selection range yielded higher coverage depth with sufficient numbers of loci and was used in all future library preparations.

Stacks Parameter Optimization—

A *Stacks 2.0* wrapper script (*denovo_map.pl*) tested parameter settings on clustering of reads into putative loci (i.e., M=n for values equal to 1–9 while maintaining m=3). Once *denovo_map.pl* was completed for all parameter combinations, the *populations* module was re-run to retain only loci genotyped in at least 80% of samples (Paris et al., 2017). A script (Nicolas Rochette; bitbucket.org/rochette/rad-seq-genotyping-demo/src/) extracted loci and SNPs from each parameter value combination. Three response variables were plotted against parameter value combinations for each sample subset, including: (1) loci retained by at least 80% of samples, (2) new loci added to the *Stacks 2.0* catalog and present in at least 80% of samples, and (3) distribution of SNPs per locus. Plots were evaluated to identify the parameter values at which the number of polymorphic loci and number of SNPs shared by at least 80% of samples stabilized (Paris et al., 2017).

The protocol was performed on two different sample sets to confirm that selection did not impact optimization. Samples were selected to be representative of the entire data set by including samples: (a) Of each tissue type, (b) collected throughout the length of the study, and (c) digested, ligated, and sequenced in different batches. Care was taken to ensure that no duplicates were included (see above). When performed on both sets, the protocol resulted in consistent identification of optimal clustering parameters [m=3, M=2, n=2].

Pedigree Confidence—

Accuracy of the reconstructed pedigree was assessed in three ways. First, *Sequoia's EstConf* function was used to calculate confidence probabilities of parentage assignments for dams and sires of known ID (TABLE S1). Simulations were run for 50 iterations (*nSim*=50) and assumed that 40% of parents were not sampled (*ParMis*=0.4). Second, pairwise pedigree relatedness [as estimated from the reconstructed *Sequoia* pedigree using the *R* package *Pedantics* (Morrissey & Wilson, 2010)] was regressed onto pairwise genomic relatedness [estimated using Wang's estimator corrected for small sample size (Wang, 2017) in the *R* package *irelr* (Goncalzes & Russelo, 2011)]. Pairwise genomic relatedness was gauged from the entire set of 6,180 SNPs originally identified by the *populations* module in *Stacks 2.0*. A strong correlation between estimated pedigree relatedness and estimated pairwise genomic relationship from the complete set of markers provided support for the inferred pedigree (Huisman, 2017; FIGURE S1). Third, we also tested the ability of *Sequoia* to identify duplicate individuals by running it on data with duplicate individuals intentionally included, and found they were correctly flagged (not shown). *Sequoia* and *irelr* analyses were conducted with *R v. 3.4.3*, with *Pedantics* analyses in *RStudio* (RStudio Team, 2015) with *R v. 3.5.0*.

Supplemental Figures and Tables—

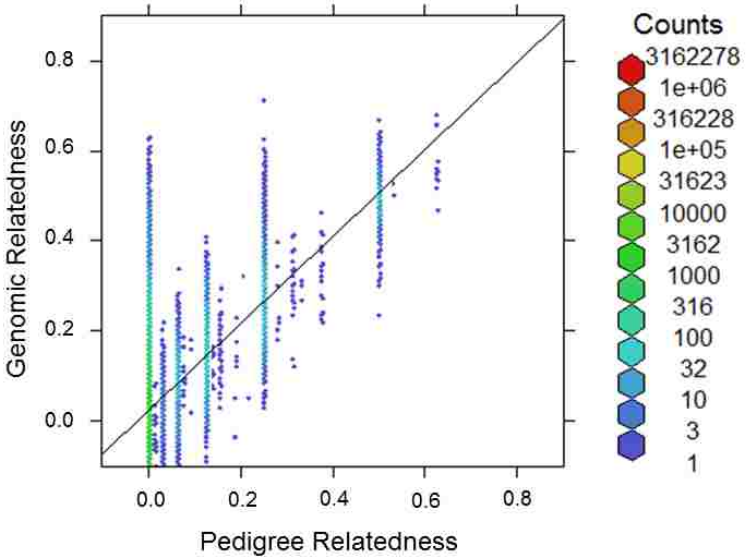

FIGURE S1. Regression of genomic relatedness (vertical axis) as estimated with the *R* package *irelr* versus pedigree relatedness (horizontal axis) as estimated from a reconstructed multigenerational pedigree using the *R* package *Pedantics* for Brown Treesnake (*Boiga irregularis*=BTS) from an experimentally-closed population on Guam (N=426). Colors identify count number.

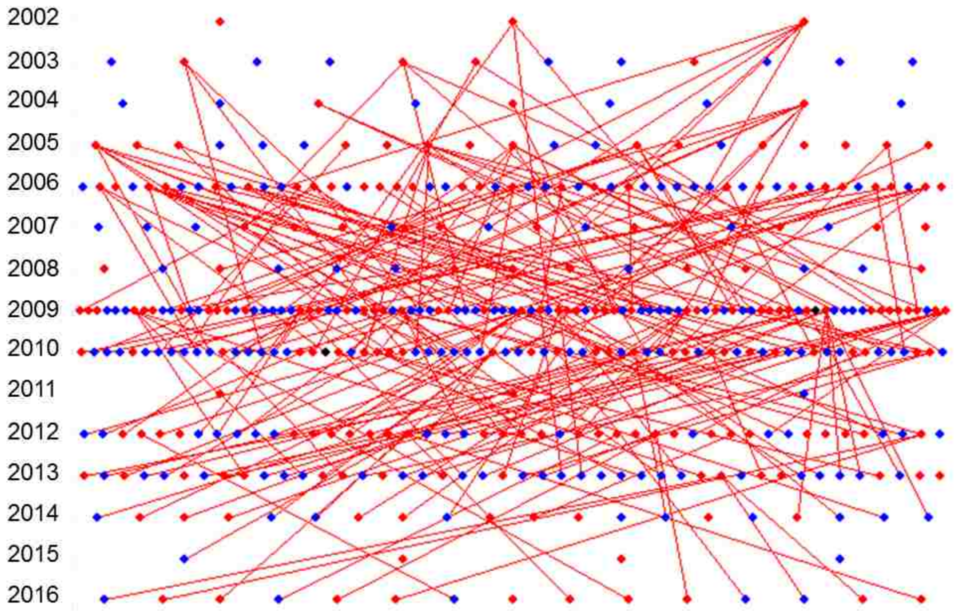

FIGURE S2. A multigenerational pedigree of an experimentally-closed population of Brown Treesnake (*Boiga irregularis*) (N=426) reconstructed from 654 SNPs (single nucleotide polymorphisms) with high minor allele frequencies (≥0.3). Only female links are shown. Vertical axis=years covered by the pedigree. Red dots represent the births of females (N=217), with red lines linking them to offspring. Blue dots represent male births (N=207). Black dots represent births of individuals with unknown sex (N=2).

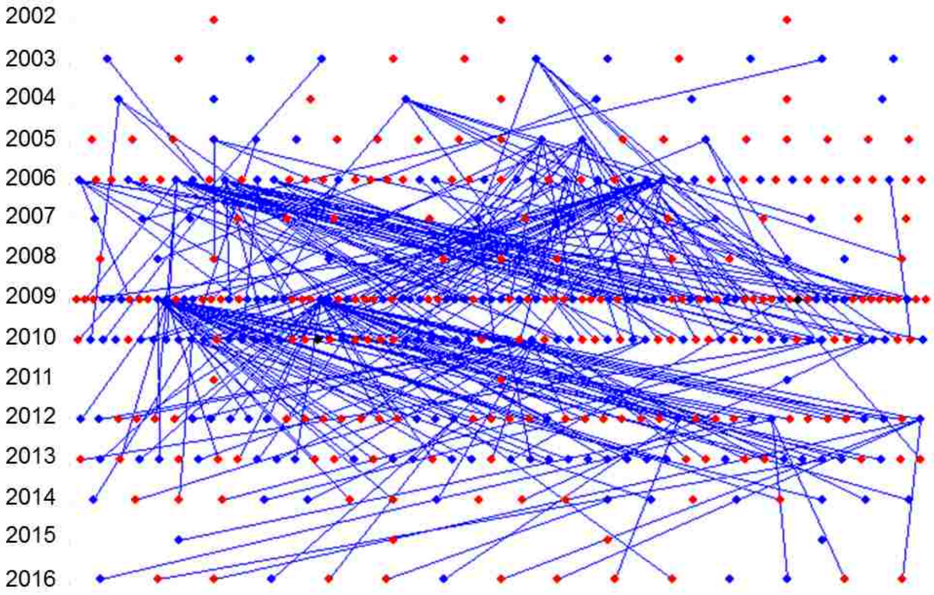

FIGURE S3. A multigenerational pedigree of an experimentally-closed population of Brown Treesnake (*Boiga irregularis*) (N=426) reconstructed from 654 SNPs (single nucleotide polymorphisms) with high minor allele frequencies (≥0.3). Only male links are shown. Vertical axis=years covered by the pedigree. Blue dots represent male births (N =207), with blue lines linking them to offspring. Red dots represent female births (N=217). Black dots represent births of individuals with unknown sex (N=2).

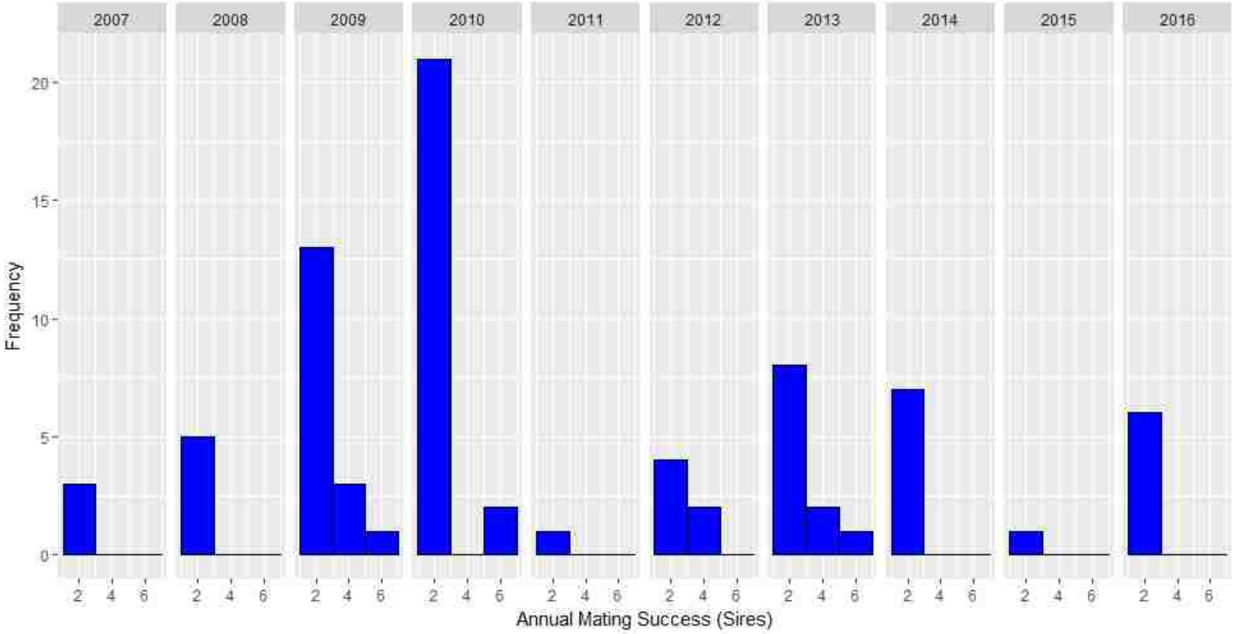

FIGURE S4. Histogram of annual mating success (= number of mating partners with which an individual produced offspring during a year) of male Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

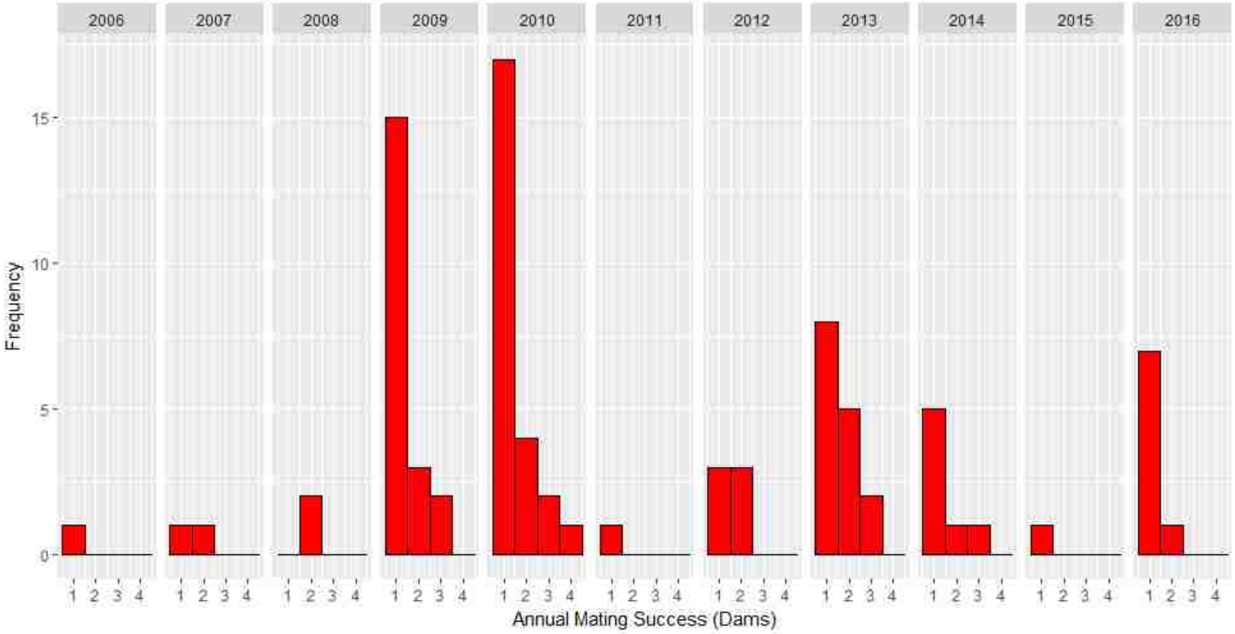

FIGURE S5. Histogram of annual mating success (= number of mating partners with which an individual produced offspring during a year) of female Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

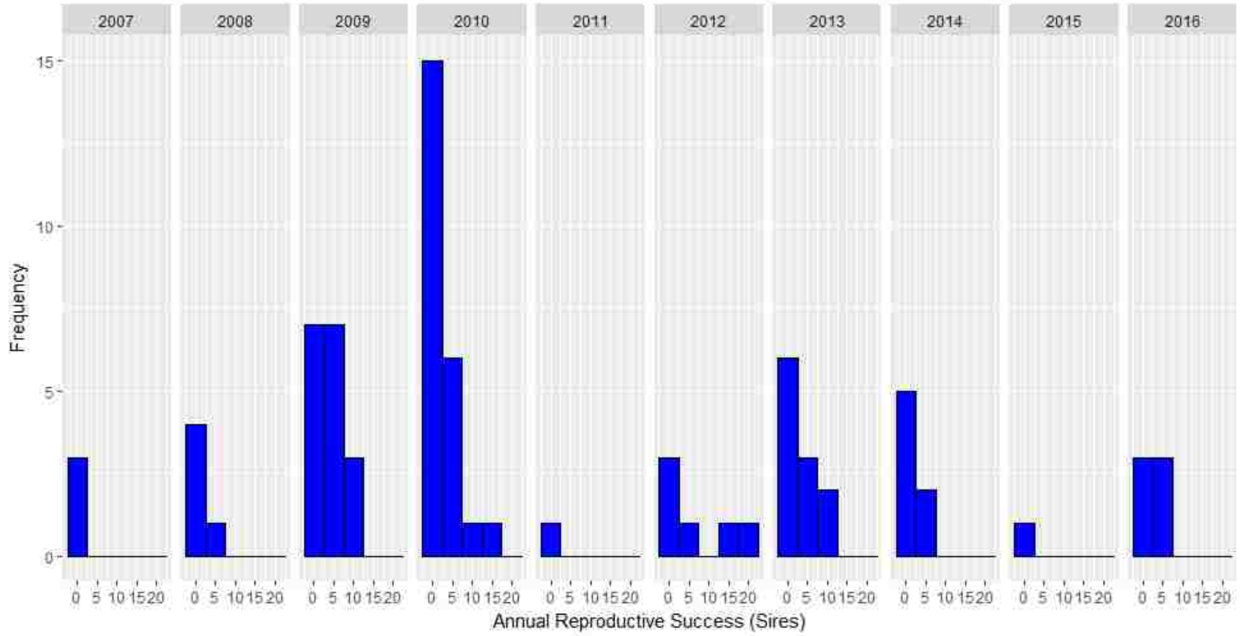

FIGURE S6. Histogram of annual reproductive success (= number of offspring produced by the individual during a year) of male Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

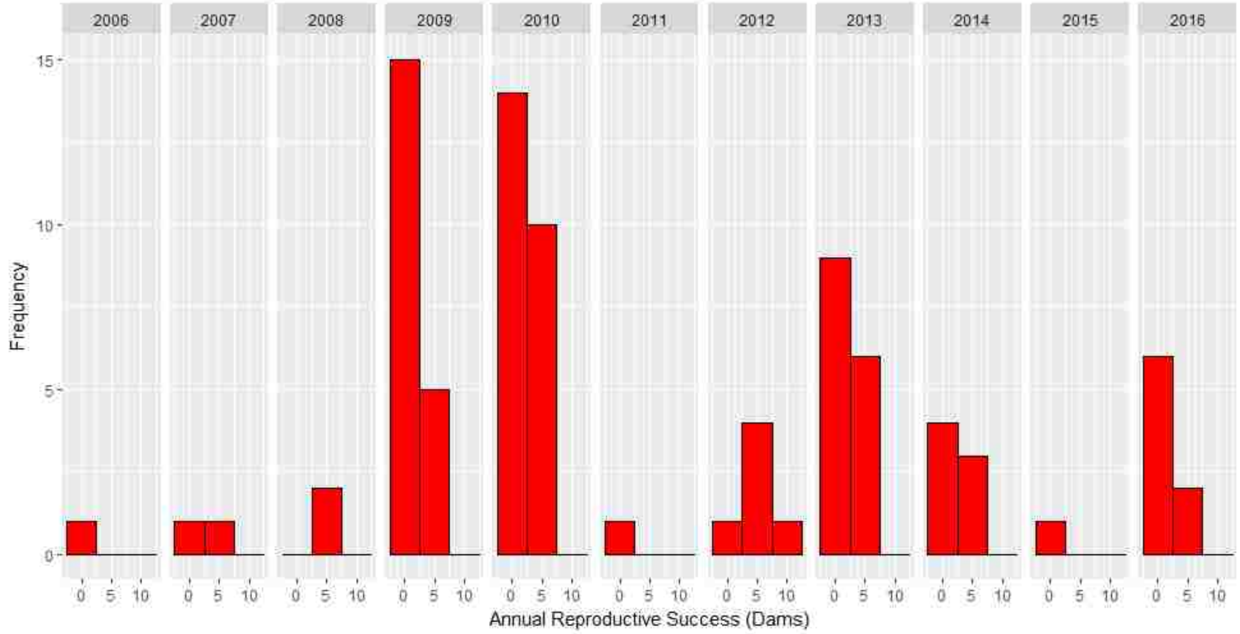

FIGURE S7. Histogram of annual reproductive success (= number of offspring produced by the individual during a year) of female Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

TABLE S1. Confidence probabilities of parentage by dams and sires of known ID (no dummy individuals) for Brown Treesnake (*Boiga irregularis*) sampled from an experimentally-closed population on Guam (N=426) and estimated with the *EstConf* function of the *R* package *Sequoia*. *EstConf* was run for 50 iterations (*nSim*=50), and simulations assumed that 40% of parents were not sampled (*ParMis*=0.4). ID=individual sample; Dam=mother of known ID; Dam probability=probability of maternity; Sire=father of known ID; Sire Probability=probability of paternity.

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS001	-	-	-	-
13BTS002	-	-	-	-
13BTS003	-	-	-	-
13BTS004	-	-	-	-
13BTS005	-	-	-	-
13BTS006	-	-	-	-
13BTS007	-	-	13BTS095	0.99026
13BTS008	-	-	-	-
13BTS009	-	-	-	-
13BTS010	-	-	-	-
13BTS011	13BTS039	0.93149	13BTS068	0.99026
13BTS012	-	-	-	-
13BTS013	-	-	-	-
13BTS014	-	-	-	-
13BTS015	-	-	-	-
13BTS016	-	-	-	-
13BTS017	-	-	-	-
13BTS018	-	-	13BTS022	0.99026
13BTS019	-	-	-	-
13BTS020	-	-	-	-
13BTS021	13BTS020	0.97397	-	-
13BTS022	-	-	-	-
13BTS023	-	-	-	-
13BTS024	-	-	-	-
13BTS025	-	-	13BTS103	0.99026
13BTS026	-	-	-	-
13BTS027	-	-	-	-
13BTS028	-	-	-	-
13BTS029	-	-	-	-
13BTS030	13BTS125	0.93149	13BTS023	0.99026
13BTS031	-	-	-	-
13BTS032	-	-	-	-
13BTS033	-	-	-	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS034	-	-	-	-
13BTS035	-	-	-	-
13BTS036	-	-	-	-
13BTS037	13BTS082	-	-	-
13BTS038	-	-	-	-
13BTS039	-	-	-	-
13BTS040	-	-	-	-
13BTS041	-	-	-	-
13BTS042	-	-	-	-
13BTS043	-	-	-	-
13BTS044	-	-	-	-
13BTS046	13BTS082	-	13BTS058	-
13BTS047	-	-	-	-
13BTS048	-	-	-	-
13BTS049	-	-	-	-
13BTS050	-	-	-	-
13BTS051	13BTS082	-	-	-
13BTS052	-	-	-	-
13BTS053	-	-	-	-
13BTS054	-	-	-	-
13BTS055	-	-	-	-
13BTS056	-	-	-	-
13BTS057	-	-	-	-
13BTS058	-	-	-	-
13BTS059	-	-	-	-
13BTS060	-	-	-	-
13BTS061	-	-	-	-
13BTS062	-	-	-	-
13BTS063	13BTS082	-	-	-
13BTS064	-	-	-	-
13BTS065	-	-	-	-
13BTS066	-	-	-	-
13BTS067	-	-	-	-
13BTS068	-	-	-	-
13BTS069	-	-	-	-
13BTS070	13BTS020	0.97397	-	-
13BTS072	-	-	-	-
13BTS073	-	-	-	-
13BTS074	-	-	-	-
13BTS075	-	-	-	-
13BTS077	-	-	-	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS078	-	-	-	-
13BTS079	-	-	-	-
13BTS080	-	-	-	-
13BTS081	-	-	-	-
13BTS082	-	-	-	-
13BTS083	-	-	-	-
13BTS084	-	-	-	-
13BTS085	-	-	13BTS087	0.99026
13BTS086	-	-	-	-
13BTS087	-	-	-	-
13BTS088	-	-	13BTS087	0.99026
13BTS089	-	-	-	-
13BTS091	-	-	-	-
13BTS092	-	-	-	-
13BTS093	-	-	-	-
13BTS094	-	-	-	-
13BTS095	-	-	-	-
13BTS096	-	-	-	-
13BTS097	-	-	-	-
13BTS098	-	-	-	-
13BTS099	-	-	-	-
13BTS100	-	-	-	-
13BTS101	-	-	-	-
13BTS102	-	-	-	-
13BTS103	-	-	-	-
13BTS104	13BTS125	0.93149	-	-
13BTS105	-	-	-	-
13BTS106	-	-	-	-
13BTS107	-	-	-	-
13BTS108	-	-	-	-
13BTS109	-	-	-	-
13BTS110	-	-	-	-
13BTS111	-	-	-	-
13BTS112	-	-	-	-
13BTS113	-	-	-	-
13BTS114	-	-	-	-
13BTS115	-	-	-	-
13BTS117	-	-	-	-
13BTS118	-	-	-	-
13BTS119	-	-	-	-
13BTS120	-	-	-	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS121	-	-	-	-
13BTS122	-	-	-	-
13BTS123	-	-	-	-
13BTS124	-	-	-	-
13BTS125	-	-	-	-
13BTS126	-	-	-	-
13BTS127	13BTS117	0.97397	13BTS019	-
13BTS128	-	-	-	-
13BTS129	-	-	-	-
13BTS130	-	-	-	-
13BTS131	-	-	-	-
13BTS132	-	-	-	-
13BTS133	-	-	-	-
13BTS134	-	-	13BTS002	0.99026
13BTS135	-	-	-	-
13BTS136	-	-	-	-
13BTS137	-	-	-	-
13BTS138	13BTS064	0.93149	13BTS072	0.99026
13BTS140	13BTS075	0.97397	13BTS073	0.99026
13BTS141	13BTS120	0.93149	13BTS022	0.99026
13BTS142	-	-	-	-
13BTS143	13BTS013	0.97397	13BTS102	0.99026
13BTS144	-	-	-	-
13BTS145	13BTS075	0.97397	-	-
13BTS146	-	-	13BTS041	0.99026
13BTS147	-	-	13BTS069	0.96583
13BTS148	13BTS125	0.93149	-	-
13BTS149	13BTS082	0.93149	13BTS031	0.96583
13BTS150	13BTS115	0.93149	13BTS031	0.96583
13BTS151	-	-	13BTS002	0.99026
13BTS152	-	-	-	-
13BTS153	-	-	-	-
13BTS154	-	-	-	-
13BTS155	-	-	13BTS073	0.99026
13BTS156	13BTS060	0.93149	13BTS087	0.99026
13BTS157	13BTS065	-	13BTS041	-
13BTS158	-	-	13BTS086	0.99026
13BTS159	-	-	13BTS002	-
13BTS160	-	-	-	-
13BTS161	-	-	-	-
13BTS162	-	-	-	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS163	-	-	-	-
13BTS164	13BTS016	0.93149	13BTS022	0.99026
13BTS165	-	-	-	-
13BTS166	-	-	-	-
13BTS167	-	-	13BTS073	0.99026
13BTS168	13BTS060	0.93149	13BTS084	-
13BTS169	-	-	-	-
13BTS170	-	-	13BTS086	0.99026
13BTS171	-	-	13BTS069	0.96583
13BTS172	-	-	-	-
13BTS173	-	-	13BTS102	0.99026
13BTS174	-	-	13BTS069	0.96583
13BTS175	-	-	13BTS101	0.96583
13BTS176	13BTS039	0.93149	13BTS031	0.96583
13BTS177	13BTS033	0.93149	13BTS069	0.96583
13BTS178	13BTS013	0.97397	13BTS102	0.99026
13BTS179	13BTS065	0.93149	13BTS069	0.96583
13BTS180	-	-	13BTS073	0.99026
13BTS181	13BTS020	0.97397	13BTS037	0.99026
13BTS182	-	-	-	-
13BTS183	13BTS082	0.93149	13BTS031	0.96583
13BTS184	-	-	13BTS002	0.99026
13BTS185	13BTS013	0.97397	13BTS091	0.99026
13BTS186	13BTS039	0.93149	13BTS068	0.99026
13BTS187	13BTS133	0.97397	13BTS101	0.96583
13BTS188	13BTS120	0.93149	13BTS022	0.99026
13BTS189	-	-	13BTS069	-
13BTS190	13BTS120	0.93149	13BTS022	0.99026
13BTS191	13BTS080	0.97397	13BTS086	0.99026
13BTS192	13BTS079	0.97397	13BTS073	0.99026
13BTS193	-	-	13BTS022	-
13BTS194	13BTS197	0.97397	13BTS073	0.99026
13BTS195	13BTS013	0.97397	13BTS102	0.99026
13BTS196	13BTS035	0.97397	13BTS101	0.96583
13BTS197	-	-	-	-
13BTS198	13BTS107	0.93149	13BTS022	0.99026
13BTS199	13BTS038	-	13BTS101	0.96583
13BTS200	13BTS003	-	13BTS024	-
13BTS201	-	-	13BTS069	0.96583
13BTS202	-	-	13BTS031	0.96583
13BTS203	13BTS010	0.97397	13BTS101	0.96583

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS204	13BTS125	0.93149	13BTS084	-
13BTS205	13BTS013	0.97397	13BTS102	0.99026
13BTS206	13BTS125	0.93149	13BTS102	0.99026
13BTS207	13BTS098	0.97397	13BTS023	0.99026
13BTS208	13BTS016	0.93149	13BTS022	0.99026
13BTS209	13BTS096	0.93149	13BTS022	0.99026
13BTS210	-	-	13BTS073	0.99026
13BTS214	13BTS050	-	13BTS102	0.99026
13BTS215	13BTS055	-	13BTS037	0.99026
13BTS216	13BTS115	0.93149	13BTS036	0.99026
13BTS217	13BTS009	0.97397	13BTS101	0.96583
13BTS218	13BTS079	0.97397	13BTS031	0.96583
13BTS219	-	-	-	-
13BTS220	13BTS012	-	13BTS069	0.96583
13BTS221	13BTS133	0.97397	13BTS101	0.96583
13BTS222	-	-	13BTS022	0.99026
13BTS223	-	-	13BTS101	0.96583
13BTS224	13BTS020	0.97397	13BTS069	0.96583
13BTS225	13BTS109	0.97397	13BTS031	0.96583
13BTS226	-	-	13BTS037	0.99026
13BTS227	13BTS056	0.97397	13BTS031	0.96583
13BTS230	13BTS003	-	13BTS051	-
13BTS231	-	-	13BTS101	0.96583
13BTS232	13BTS075	0.97397	-	-
13BTS234	13BTS075	0.97397	13BTS073	0.99026
13BTS235	-	-	13BTS005	0.99026
13BTS236	13BTS065	0.93149	-	-
13BTS237	13BTS060	0.93149	13BTS073	0.99026
13BTS238	13BTS079	0.97397	13BTS073	0.99026
13BTS239	13BTS064	-	13BTS072	-
13BTS240	-	-	13BTS101	0.96583
13BTS241	13BTS060	0.93149	13BTS087	0.99026
13BTS242	13BTS010	0.97397	13BTS101	0.96583
13BTS243	-	-	13BTS022	0.99026
13BTS244	13BTS009	0.97397	13BTS101	0.96583
13BTS246	13BTS060	-	13BTS073	-
13BTS247	13BTS010	0.97397	13BTS101	0.96583
13BTS248	13BTS003	0.97397	13BTS006	0.99026
13BTS249	13BTS021	0.97397	13BTS031	0.96583
13BTS253	13BTS015	0.93149	13BTS031	0.96583
13BTS254	13BTS064	0.93149	13BTS072	0.99026

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS255	13BTS009	0.97397	13BTS101	0.96583
13BTS256	-	-	13BTS087	0.99026
13BTS257	13BTS133	0.97397	13BTS046	0.96583
13BTS258	13BTS107	-	13BTS022	-
13BTS259	-	-	13BTS086	0.99026
13BTS260	-	-	13BTS101	-
13BTS261	13BTS125	0.93149	-	-
13BTS262	13BTS015	0.93149	13BTS031	0.96583
13BTS263	-	-	-	-
13BTS264	-	-	13BTS006	0.99026
13BTS265	13BTS049	0.97397	13BTS087	0.99026
13BTS267	-	-	13BTS084	-
13BTS268	13BTS010	0.97397	13BTS054	-
13BTS269	13BTS010	0.97397	13BTS052	-
13BTS270	-	-	13BTS031	0.96583
13BTS271	-	-	-	-
13BTS272	-	-	13BTS101	-
13BTS273	13BTS065	0.93149	13BTS091	0.99026
13BTS274	13BTS065	0.93149	13BTS091	0.99026
13BTS276	-	-	-	-
13BTS278	13BTS048	-	13BTS086	0.99026
13BTS280	13BTS065	0.93149	13BTS091	0.99026
13BTS281	13BTS125	-	13BTS037	-
13BTS283	13BTS114	0.97397	13BTS077	0.99026
13BTS284	-	-	13BTS046	0.96583
13BTS285	13BTS133	0.97397	13BTS046	0.96583
13BTS287	13BTS060	0.93149	13BTS073	0.99026
13BTS288	13BTS189	0.93149	13BTS141	0.99026
13BTS289	-	-	-	-
13BTS290	-	-	-	-
13BTS291	13BTS033	0.93149	13BTS058	0.96583
13BTS293	-	-	-	-
13BTS294	-	-	-	-
13BTS295	13BTS033	0.93149	13BTS058	0.96583
13BTS296	-	-	13BTS031	0.96583
13BTS297	-	-	13BTS101	0.96583
13BTS298	-	-	13BTS002	0.99026
13BTS299	13BTS010	0.97397	13BTS101	0.96583
13BTS301	13BTS107	0.93149	13BTS022	0.99026
13BTS302	13BTS075	0.97397	13BTS023	0.99026
13BTS303	-	-	13BTS087	0.99026

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS304	-	-	13BTS002	0.99026
13BTS305	-	-	-	-
13BTS308	13BTS114	0.97397	13BTS077	0.99026
13BTS310	-	-	13BTS006	0.99026
13BTS311	13BTS015	0.93149	13BTS031	0.96583
13BTS315	-	-	13BTS058	0.96583
13BTS316	13BTS096	0.93149	13BTS022	0.99026
13BTS317	13BTS081	-	13BTS058	-
13BTS318	-	-	13BTS054	-
13BTS320	-	-	-	-
13BTS322	-	-	13BTS037	0.99026
13BTS323	13BTS174	0.97397	13BTS260	0.96583
13BTS324	13BTS159	0.93149	13BTS260	0.96583
13BTS325	13BTS081	0.97397	13BTS058	0.96583
13BTS326	13BTS119	0.97397	13BTS022	0.99026
13BTS328	-	-	13BTS162	0.99026
13BTS332	13BTS189	0.93149	13BTS141	0.99026
13BTS334	13BTS029	0.97397	13BTS102	0.99026
13BTS338	-	-	13BTS162	0.99026
13BTS339	-	-	-	-
13BTS342	13BTS159	0.93149	13BTS260	0.96583
13BTS343	13BTS159	0.93149	13BTS162	0.99026
13BTS346	13BTS174	0.97397	13BTS162	0.99026
13BTS348	13BTS174	0.97397	13BTS162	0.99026
13BTS349	-	-	-	-
13BTS351	-	-	13BTS141	0.99026
13BTS352	13BTS207	0.97397	13BTS162	0.99026
13BTS359	13BTS287	0.97397	13BTS311	0.99026
13BTS360	-	-	13BTS246	0.96583
13BTS361	13BTS270	0.97397	13BTS206	0.99026
13BTS362	13BTS191	0.97397	13BTS141	0.99026
13BTS363	13BTS189	0.93149	13BTS141	0.99026
13BTS364	13BTS278	0.97397	13BTS200	0.96583
13BTS365	13BTS270	0.97397	13BTS162	0.99026
13BTS366	13BTS255	0.97397	13BTS281	0.96583
13BTS367	13BTS239	0.93149	13BTS140	0.99026
13BTS368	13BTS189	0.93149	13BTS141	0.99026
13BTS369	13BTS189	0.93149	13BTS141	0.99026
13BTS370	-	-	13BTS190	0.99026
13BTS371	-	-	13BTS162	0.99026
13BTS372	13BTS222	0.97397	13BTS162	0.99026

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS373	13BTS189	0.93149	13BTS141	0.99026
13BTS374	13BTS339	0.93149	13BTS141	0.99026
13BTS377	13BTS174	0.97397	13BTS162	0.99026
13BTS378	-	-	-	-
13BTS379	13BTS339	0.93149	13BTS260	0.96583
13BTS381	13BTS339	0.93149	13BTS141	0.99026
13BTS382	13BTS296	0.97397	13BTS141	0.99026
13BTS383	13BTS134	0.97397	13BTS162	0.99026
13BTS384	13BTS270	0.97397	13BTS236	0.99026
13BTS385	13BTS287	0.97397	13BTS258	0.96583
13BTS388	13BTS278	0.97397	13BTS200	0.96583
13BTS391	13BTS134	0.97397	13BTS162	0.99026
13BTS395	13BTS255	0.97397	13BTS140	0.99026
13BTS398	13BTS272	0.93149	13BTS311	0.99026
13BTS399	13BTS255	0.97397	13BTS325	0.99026
13BTS400	13BTS204	0.97397	13BTS260	0.96583
13BTS402	13BTS174	0.97397	13BTS162	0.99026
13BTS403	13BTS540	0.97397	13BTS140	0.99026
13BTS404	13BTS255	0.97397	13BTS281	0.96583
13BTS405	-	-	13BTS140	0.99026
13BTS406	13BTS272	0.93149	13BTS140	0.99026
13BTS407	13BTS174	0.97397	13BTS162	0.99026
13BTS408	13BTS339	0.93149	13BTS260	0.96583
13BTS409	-	-	13BTS141	0.99026
13BTS410	13BTS222	0.97397	13BTS162	0.99026
13BTS413	13BTS134	0.97397	13BTS162	0.99026
13BTS414	13BTS222	0.97397	13BTS260	0.96583
13BTS417	-	-	13BTS246	0.96583
13BTS419	13BTS159	0.93149	13BTS141	0.99026
13BTS421	13BTS296	0.97397	13BTS141	0.99026
13BTS422	13BTS193	0.93149	13BTS260	0.96583
13BTS423	13BTS540	0.97397	13BTS267	-
13BTS425	13BTS317	-	13BTS258	0.96583
13BTS429	-	-	13BTS162	0.99026
13BTS430	-	-	13BTS162	0.99026
13BTS431	13BTS222	0.97397	13BTS140	0.99026
13BTS436	13BTS191	0.97397	13BTS140	0.99026
13BTS439	-	-	13BTS260	-
13BTS440	-	-	13BTS162	0.99026
13BTS441	13BTS193	0.93149	13BTS140	0.99026
13BTS442	13BTS339	-	13BTS141	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS444	-	-	-	-
13BTS445	13BTS159	0.93149	13BTS246	0.96583
13BTS457	13BTS134	0.97397	13BTS162	0.99026
13BTS460	-	-	13BTS236	0.99026
13BTS468	13BTS222	0.97397	13BTS140	0.99026
13BTS472	13BTS261	0.97397	13BTS260	0.96583
13BTS500	-	-	-	-
13BTS501	13BTS517	0.97397	13BTS325	0.99026
13BTS503	-	-	-	-
13BTS504	13BTS255	0.97397	13BTS140	0.99026
13BTS510	13BTS193	0.93149	13BTS140	0.99026
13BTS514	13BTS235	0.97397	13BTS190	0.99026
13BTS517	-	-	13BTS162	0.99026
13BTS518	-	-	-	-
13BTS521	13BTS372	0.97397	13BTS527	-
13BTS525	-	-	-	-
13BTS526	-	-	13BTS260	0.96583
13BTS527	13BTS339	-	13BTS141	-
13BTS529	13BTS189	0.93149	13BTS141	0.99026
13BTS532	-	-	13BTS141	0.99026
13BTS535	13BTS278	0.97397	13BTS200	0.96583
13BTS540	13BTS033	0.93149	13BTS121	0.99026
13BTS543	-	-	-	-
13BTS548	-	-	-	-
13BTS549	-	-	-	-
13BTS551	13BTS526	0.97397	13BTS529	0.99026
13BTS553	13BTS056	0.97397	13BTS031	0.96583
13BTS556	-	-	13BTS162	0.99026
13BTS557	13BTS174	0.97397	13BTS162	0.99026
13BTS558	13BTS207	0.97397	13BTS162	0.99026
13BTS559	-	-	-	-
13BTS561	13BTS272	0.93149	13BTS140	0.99026
13BTS562	13BTS287	0.97397	13BTS258	0.96583
13BTS563	13BTS174	0.97397	13BTS162	0.99026
13BTS565	13BTS278	0.97397	13BTS200	0.96583
13BTS566	13BTS189	0.93149	13BTS141	0.99026
13BTS571	-	-	13BTS260	0.96583
13BTS574	13BTS191	0.97397	13BTS140	0.99026
13BTS575	13BTS193	0.93149	13BTS162	0.99026
13BTS576	13BTS272	-	13BTS162	-
13BTS577	13BTS566	0.97397	13BTS576	-

Table S1 (Cont.)

ID	Dam	Dam Probability	Sire	Sire Probability
13BTS588	-	-	-	-
13BTS591	13BTS272	0.93149	13BTS162	0.99026
13BTS597	13BTS239	0.93149	13BTS260	0.96583
13BTS598	13BTS239	0.93149	13BTS140	0.99026
13BTS601	13BTS372	0.97397	13BTS608	0.99026
13BTS602	-	-	-	-
13BTS603	13BTS429	0.97397	13BTS377	0.99026
13BTS605	13BTS439	0.93149	13BTS377	0.99026
13BTS607	13BTS566	0.97397	13BTS518	-
13BTS608	-	-	13BTS162	0.99026
13BTS609	13BTS328	0.97397	13BTS442	0.96583
13BTS620	13BTS270	0.97397	13BTS236	0.99026
13BTS621	-	-	-	-
13BTS625	-	-	-	-
13BTS630	-	-	13BTS608	0.99026
13BTS634	13BTS372	0.97397	13BTS608	0.99026
13BTS640	13BTS272	0.93149	13BTS236	0.99026
13BTS641	13BTS368	0.97397	13BTS442	0.96583
13BTS643	13BTS439	0.93149	13BTS377	0.99026
13BTS649	13BTS261	0.97397	-	-
13BTS662	13BTS526	0.97397	13BTS529	0.99026
13BTS664	13BTS526	0.97397	13BTS529	0.99026
13BTS670	-	-	13BTS267	-

Table S2. Candidate generalized linear mixed models of male Brown Treesnake (*Boiga irregularis*) annual mating success were compared and ranked with Akaike Information Criteria as corrected for small sample size (AICc) using the *dredge* function of the *R* package *MuMIn*. Models are ranked from greatest (=top) to least (=bottom) support, with the top model in bold. GLMM parameter estimates are presented for fixed effects (i.e., 'Intercept', 'Age', 'BCI'=Body Condition Index, 'Trappability', and 'Inbreeding') in a candidate model. 'Model'=model number; 'K'=number of model parameters; 'LogLik'=log-likelihood of candidate model; 'ΔAICc'=delta AICc; 'Weight'=AICc model weight.

Model	Intercept	Age	BCI	Trappability	Inbreeding	K	LogLik	AICc	ΔAICc	Weight
8	**-5.78**	**0.50**	**5.48**	**0.13**	**-**	**6**	**-221.90**	**455.94**	**0.00**	**0.73**
16	-5.78	0.50	5.48	0.13	0.03	7	-221.90	457.98	2.04	0.26
4	-5.37	0.53	5.65	-	-	5	-228.72	467.53	11.59	0.00
12	-5.36	0.53	5.62	-	-0.50	6	-228.64	469.41	13.47	0.00
7	-4.69	-	6.33	0.17	-	5	-233.71	477.51	21.57	0.00
15	-4.69	-	6.27	0.17	-0.78	6	-233.53	479.19	23.26	0.00
6	-7.09	0.71	-	0.16	-	5	-236.59	483.27	27.33	0.00
14	-7.08	0.70	-	0.16	-0.52	6	-236.54	485.21	29.28	0.00
3	-4.17	-	6.42	-	-	4	-243.38	494.82	38.88	0.00
11	-4.18	-	6.31	-	-1.28	5	-242.85	495.78	39.85	0.00
2	-6.53	0.73	-	-	-	4	-246.14	500.34	44.41	0.00
10	-6.49	0.71	-	-	-1.26	5	-245.84	501.77	45.83	0.00
13	-5.52	-	-	0.19	-2.55	5	-256.09	522.27	66.33	0.00
5	-5.48	-	-	0.20	-	4	-257.25	522.57	66.63	0.00
9	-4.94	-	-	-	-3.16	4	-267.79	543.64	87.70	0.00
1	-4.90	-	-	-	-	3	-269.81	545.65	89.71	0.00

Table S3. Candidate generalized linear mixed models of female Brown Treesnake (*Boiga irregularis*) annual mating success were compared and ranked with Akaike Information Criteria as corrected for small sample size (AICc) using the *dredge* function of the *R* package *MuMIn*. Models are ranked from greatest (=top) to least (=bottom) support, with the top two models that were averaged in bold. GLMM parameter estimates are presented for fixed effects (i.e., ’Intercept’, ‘Age’, ‘BCI’=Body Condition Index, ‘Trappability’, and ‘Inbreeding’) in a candidate model. ‘Model’=model number; ‘K’=number of model parameters; ‘LogLik’=log-likelihood of candidate model; ‘ΔAICc’=delta AICc; ‘Weight’=AICc model weight.

Model	Intercept	Age	BCI	Trappability	Inbreeding	K	LogLik	AICc	ΔAICc	Weight
8	**-5.63**	**0.50**	**2.63**	**0.06**	**-**	**6**	**-223.96**	**460.03**	**0.00**	**0.60**
16	**-5.61**	**0.50**	**2.61**	**0.06**	**-0.88**	**7**	**-223.74**	**461.63**	**1.60**	**0.27**
4	-5.63	0.54	2.53	-	-	5	-226.92	463.92	3.89	0.09
12	-5.61	0.54	2.51	-	-0.76	6	-226.75	465.61	5.58	0.04
6	-5.87	0.54	-	0.05	-	5	-229.32	468.73	8.70	0.01
14	-5.83	0.53	-	0.05	-1.10	6	-228.99	470.10	10.06	0.00
2	-5.87	0.57	-	-	-	4	-232.04	472.14	12.11	0.00
10	-5.84	0.57	-	-	-1.01	5	-231.75	473.59	13.56	0.00
7	-4.19	-	2.83	0.09	-	5	-242.47	495.02	34.98	0.00
15	-4.17	-	2.80	0.09	-1.97	6	-241.47	495.06	35.03	0.00
3	-4.04	-	2.76	-	-	4	-249.42	506.89	46.85	0.00
11	-4.03	-	2.73	-	-1.88	5	-248.50	507.07	47.04	0.00
13	-4.28	-	-	0.09	-2.13	5	-248.69	507.47	47.43	0.00
5	-4.30	-	-	0.09	-	4	-249.91	507.88	47.85	0.00
9	-4.16	-	-	-	-2.10	4	-255.51	519.07	59.04	0.00
1	-4.17	-	-	-	-	3	-256.69	519.41	59.38	0.00

Table S4. Candidate generalized linear mixed models of male Brown Treesnake (*Boiga irregularis*) annual reproductive success were compared and ranked with Akaike Information Criteria as corrected for small sample size (AICc) using the *dredge* function of the *R* package *MuMIn*. Models are ranked from greatest (=top) to least (=bottom) support, with the top four models that were averaged in bold. GLMM parameter estimates are presented for fixed effects (i.e., 'Intercept', 'Age', 'BCI'=Body Condition Index, 'Trappability', 'Inbreeding', and 'MS'=Mating Success) in a candidate model. 'Model'=model number; 'K'=number of model parameters; 'LogLik'=log-likelihood of candidate model; 'ΔAICc'=delta AICc; 'Weight'=AICc model weight.

Model	Intercept	Age	BCI	Trappability	Inbreeding	MS	K	LogLik	AICc	ΔAICc	Weight
24	**-4.81**	**0.38**	**2.48**	**0.05**	**-**	**0.92**	**7**	**-196.54**	**407.25**	**0.00**	**0.33**
20	**-4.69**	**0.39**	**2.48**	**-**	**-**	**0.94**	**6**	**-197.66**	**407.45**	**0.20**	**0.30**
28	**-4.67**	**0.39**	**2.46**	**-**	**-0.94**	**0.94**	**7**	**-197.29**	**408.76**	**1.51**	**0.15**
32	**-4.79**	**0.37**	**2.47**	**0.05**	**-0.75**	**0.92**	**8**	**-196.31**	**408.84**	**1.58**	**0.15**
22	-5.03	0.41	-	0.06	-	1.00	6	-200.03	412.18	4.93	0.03
18	-4.92	0.43	-	-	-	1.02	5	-201.21	412.51	5.26	0.02
30	-5.00	0.40	-	0.05	-0.75	1.00	7	-199.80	413.76	6.51	0.01
26	-4.89	0.42	-	-	-0.95	1.02	6	-200.83	413.80	6.54	0.01
23	-4.01	-	3.02	0.08	-	0.97	6	-204.66	421.45	14.19	0.00
31	-4.00	-	2.97	0.08	-1.10	0.97	7	-204.13	422.42	15.17	0.00
19	-3.79	-	3.01	-	-	0.99	5	-206.88	423.85	16.59	0.00
27	-3.79	-	2.94	-	-1.30	0.99	6	-206.13	424.38	17.13	0.00
21	-4.07	-	-	0.08	-	1.09	5	-209.94	429.96	22.71	0.00
29	-4.07	-	-	0.08	-1.28	1.09	6	-209.23	430.60	23.34	0.00
17	-3.87	-	-	-	-	1.11	4	-212.28	432.63	25.38	0.00
25	-3.88	-	-	-	-1.51	1.10	5	-211.31	432.70	25.45	0.00
8	-6.85	0.62	5.92	0.17	-	-	6	-263.92	539.96	132.71	0.00
16	-6.84	0.61	5.91	0.17	-0.17	-	7	-263.91	542.00	134.74	0.00
4	-6.20	0.65	6.12	-	-	-	5	-273.89	557.88	150.62	0.00
12	-6.18	0.64	6.09	-	-0.72	-	6	-273.79	559.70	152.45	0.00
7	-5.63	-	7.16	0.21	-	-	5	-277.73	565.54	158.29	0.00
15	-5.65	-	7.06	0.20	-1.41	-	6	-277.38	566.88	159.63	0.00
6	-8.72	0.92	-	0.19	-	-	5	-279.64	569.38	162.13	0.00
14	-8.69	0.91	-	0.19	-1.01	-	6	-279.54	571.22	163.96	0.00
3	-4.87	-	7.19	-	-	-	4	-291.30	590.67	183.42	0.00

Table S4 (Cont.)

Model	Intercept	Age	BCI	Trappability	Inbreeding	MS	K	LogLik	AICc	ΔAICc	Weight
11	-4.90	-	7.06	-	-1.95	-	5	-290.55	591.19	183.94	0.00
2	-7.91	0.93	-	-	-	-	4	-292.95	593.97	186.72	0.00
10	-7.85	0.91	-	-	-1.76	-	5	-292.60	595.30	188.04	0.00
13	-7.54	-	-	0.23	-5.25	-	5	-303.33	616.74	209.49	0.00
5	-7.42	-	-	0.23	-	-	4	-305.32	618.71	211.46	0.00
9	-6.64	-	-	-	-5.59	-	4	-319.29	646.64	239.38	0.00
1	-6.57	-	-	-	-	-	3	-321.91	649.85	242.60	0.00

Table S5. Candidate generalized linear mixed models of female Brown Treesnake (*Boiga irregularis*) annual reproductive success were compared and ranked with Akaike Information Criteria as corrected for small sample size (AICc) using the *dredge* function of the *R* package *MuMIn*. Models are ranked from greatest (=top) to least (=bottom) support, with the top four models that were averaged in bold. GLMM parameter estimates are presented for fixed effects (i.e., 'Intercept', 'Age', 'BCI'=Body Condition Index, 'Trappability', 'Inbreeding', and 'MS'=Mating Success) in a candidate model. 'Model'=model number; 'K'=number of model parameters; 'LogLik'=log-likelihood of candidate model; 'ΔAICc'=delta AICc; 'Weight'=AICc model weight.

Model	Intercept	Age	BCI	Trappability	Inbreeding	MS	K	LogLik	AICc	Δ AICc	Weight
30	**-5.03**	**0.28**	**-**	**0.04**	**-2.32**	**1.74**	**7**	**-202.75**	**419.65**	**0.00**	**0.20**
26	**-5.00**	**0.30**	**-**	**-**	**-2.28**	**1.81**	**6**	**-203.83**	**419.77**	**0.11**	**0.19**
18	**-5.09**	**0.31**	**-**	**-**	**-**	**1.83**	**5**	**-205.03**	**420.15**	**0.50**	**0.16**
22	**-5.11**	**0.29**	**-**	**0.04**	**-**	**1.77**	**6**	**-204.04**	**420.20**	**0.55**	**0.15**
32	-5.02	0.28	0.05	0.04	-2.31	1.74	8	-202.75	421.69	2.04	0.07
28	-5.01	0.30	-0.02	-	-2.28	1.81	7	-203.83	421.81	2.15	0.07
20	-5.08	0.31	0.03	-	-	1.83	6	-205.03	422.18	2.53	0.06
24	-5.10	0.29	0.10	0.04	-	1.77	7	-204.04	422.23	2.58	0.06
29	-4.20	-	-	0.05	-2.58	1.87	6	-206.73	425.57	5.92	0.01
25	-4.10	-	-	-	-2.56	1.99	5	-208.23	426.54	6.89	0.01
21	-4.25	-	-	0.05	-	1.91	5	-208.29	426.66	7.01	0.01
17	-4.15	-	-	-	-	2.02	4	-209.67	427.39	7.74	0.00
31	-4.19	-	0.21	0.05	-2.57	1.87	7	-206.71	427.56	7.91	0.00
27	-4.09	-	0.17	-	-2.56	1.98	6	-208.21	428.54	8.89	0.00

Table S5 (Cont.)

Model	Intercept	Age	BCI	Trappability	Inbreeding	MS	K	LogLik	AICc	Δ AICc	Weight
23	-4.23	-	0.27	0.05	-	1.91	6	-208.25	428.61	8.96	0.00
19	-4.13	-	0.24	-	-	2.02	5	-209.64	429.36	9.70	0.00
8	-6.56	0.63	3.00	0.08	-	-	6	-308.49	629.09	209.44	0.00
16	-6.50	0.62	2.98	0.08	-1.38	-	7	-308.11	630.38	210.73	0.00
6	-7.00	0.70	-	0.08	-	-	5	-315.13	640.34	220.69	0.00
4	-6.62	0.68	2.80	-	-	-	5	-315.14	640.36	220.71	0.00
14	-6.93	0.69	-	0.08	-1.71	-	6	-314.62	641.35	221.70	0.00
12	-6.57	0.68	2.78	-	-1.26	-	6	-314.83	641.77	222.12	0.00
2	-7.07	0.76	-	-	-	-	4	-321.20	650.46	230.81	0.00
10	-7.01	0.75	-	-	-1.61	-	5	-320.75	651.58	231.93	0.00
15	-4.90	-	3.54	0.11	-3.00	-	6	-329.38	670.87	251.22	0.00
7	-4.94	-	3.60	0.11	-	-	5	-330.93	671.93	252.28	0.00
13	-5.20	-	-	0.11	-3.59	-	5	-340.01	690.09	270.44	0.00
11	-4.86	-	3.40	-	-3.11	-	5	-340.57	691.23	271.58	0.00
5	-5.25	-	-	0.11	-	-	4	-342.03	692.11	272.46	0.00
3	-4.90	-	3.46	-	-	-	4	-342.12	692.29	272.63	0.00
9	-5.21	-	-	-	-3.83	-	4	-350.69	709.43	289.77	0.00
1	-5.26	-	-	-	-	-	3	-352.74	711.52	291.86	0.00

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Chapter 2: Temporal Variability in Selection on Invasive Brown Treesnake (*Boiga irregularis*) with Implications for Offspring Heterozygosity

ABSTRACT

Natural selection drives adaptive evolution, yet its strength can fluctuate in response to environmental changes over ecologically-relevant time scales. These caveats are of theoretical importance but also reflect strong practical considerations as well, such as with the control of invasive species. In this sense, management actions can modulate the strength of selection so as to manipulate the capacity of the population to cope with environmental changes. In this study, we tested for temporal variability in the strength of selection acting on traits previously identified as important for mating and reproductive success in Brown Treesnake (*Boiga irregularis*=BTS), an invasive that has exterminated endemic avifauna on Guam since its introduction ~1949. We first tested for temporal variation in the strength of selection, then juxtaposed annual estimates of selection gradients against data regarding prey availability, as impacted by BTS control. We then tested for a relationship between strength of selection and standardized multilocus heterozygosity of offspring (sMLH), as gauged by 1,060 single nucleotide polymorphisms (SNPs). We found significant temporal variation in selection on annual mating success (AMS) for both sexes as it relates to reproductive success (ARS) (all $P<0.05$). Selection gradients for AMS were significant for both sexes in each of 9 study years (all $P<0.001$). They were weakest in years associated with (or subsequent to) high prey availability (i.e., 2009–2010, 2012–2013), but strongest when prey available for adults was low (i.e., 2007–2008, 2011, 2015–2016). The female selection gradient for mating success also had a statistically significant effect on average sMLH of offspring produced during the year of selection ($P=0.036$). In this sense, heterozygosity of offspring was greater when the selection gradient for female AMS was most pronounced. Although prey suppression is an effective tool with which to dampen recruitment, low prey availability corresponded not only with female AMS

but also elevated heterozygosity of offspring. As such, it promotes genetic diversity of BTS on Guam.

INTRODUCTION

Anthropogenic Selection in Managed Populations—

Natural selection is the mechanism by which adaptive evolution occurs (Gompert et al., 2014), yet its strength, direction, and form can vary significantly over short, ecologically relevant time scales (Siepielski, Dibattista, & Carlson, 2009). In this sense, rapid environmental change within a single season can shift the relationship between a trait and its fitness, with the resulting fitness peaks being tracked via adaptive evolution or phenotypic plasticity (Reed, Schindler, & Waples, 2011).

This variability in selection is an important consideration for fisheries and wildlife, in that management itself can become an agent of selection that subsequently alters the fitness landscape of the managed species (Ashley et al., 2003). This is of particular concern for invasive species, in that control methods designed to alleviate a problem instead exert considerable selection pressure on the target species (termed “anthropogenic selection;” Santamaría & Méndez, 2012). Furthermore, if heritable genetic variation is a component of those traits being targeted by control, then adaptive evolution can be promoted. Yet, regardless of a trait's genetic architecture (i.e., heritable versus plastic), such selection has the potential to evoke micro-evolutionary change, particularly if the trait is related to fitness (Gompert et al., 2014). In this sense, the capacity of selection to (a) vary over time and (b) have broad genomic effects regardless of trait heritability, serves to emphasize that problem species can evolve quickly as a result of ongoing selection driven by control efforts (Reed et al., 2011).

Yet, predicting the manner by which control measures impact the fitness landscape can be difficult. For example, some of these may directly target specific traits (e.g., body size, boldness) that co-vary with other traits, such that selection on the target trait also promotes, by default, the evolution of a non-target trait (Walsh, Munch, Chiba, & Conover, 2006). In addition, some control methods (e.g., intense trapping) can also create secondary selective pressures (e.g., increases in prey abundance) that may favor phenotypes different from those originally being controlled. Thus, it is imperative that effects of selection, as imposed by control measures within a temporal framework, are projected forward as components of "evolutionary enlightened management" (Ashley et al., 2003). Unfortunately, the incorporation of evolutionary concepts into invasive species management has to date been difficult (Cook & Sgrò, 2017).

An Evolutionary Approach to Brown Treesnake Management—

Circa 1949, 10 or fewer Brown Treesnake (*Boiga irregularis*=BTS) were introduced to Guam as the U.S. military salvaged residual World War II materials from the island of Manus in the Admirality Archipelago (Fritts & Rodda, 1998; Richmond, Wood, Stanford, & Fisher, 2014). By 1980, the population had expanded to two million, with a peak density of 100 snakes per hectare (Rodda & Savidge, 2007). Given the resulting ecological and economic impacts, a variety of control methods have been implemented to reduce or eradicate its presence, and with mixed results. We suggest that control of BTS may improve if the evolutionary components of demography were incorporated into management. For example, reproductive ecology is fundamental to population persistence (Cole, 1954) and its various components could be utilized to promote control measures. Although the importance of employing reproductive ecology for BTS control has been reiterated for 20+ years [e.g., Engbring & Fritts (1988); Jordan & Rodda (1994); Rodda, Fritts, McCoid, & Campbell (1999); Greene & Mason (2000); Moore et al. (2005); Siegel, Aldridge, Clark, Poldemann, & Gribbins (2009)], its evolutionary impacts have not.

In pursuing this approach, we first attempted to link reproductive ecology with population persistence by identifying traits in BTS that significant impacted two fitness metrics: Annual mating success (AMS) and annual reproductive success (ARS; **CHAPTER 1**). By doing so, we found that AMS was significantly affected in both sexes by age, body condition, and trappability [i.e., propensity to enter baited traps (Le Cœur et al., 2015)]. However, effects on ARS differed by sex, with males significantly affected by age, AMS, and body condition. ARS of females was also affected by age and AMS, but with a negative effect of degree of inbreeding rather than body condition.

Yet, the relative fitness of phenotypes is context-dependent, such that the strength or direction of selection acting on a trait can be driven by changes in the environment. Changes in prey availability can impact the relative fitness of phenotypes (Edeline et al., 2007), and thus, the strength of selection acting on traits. In our study population, prey availability has varied considerably over time as a result of management actions.

To illustrate, a food supplementation experiment in 2009 provided snakes with more food than would occur under natural conditions, allowing large snakes to survive and reproduce into 2010 (Reed et al., unpublished data). However, by 2011, large snakes had become food deprived (Yackel Adams et al., unpublished data). Adults/subadults large enough to ingest rats were subsequently removed in mid-2011, with rat abundance increasing by end-of-year then declining again in 2014 due to BTS predation (Yackel Adams et al., unpublished data). These experiments are relevant to BTS control in that prey suppression by widespread rodenticide application is currently being explored as a management tool (Christy, Savidge, Yackel Adams, Gragg, & Rodda, 2017). Existing control tools, such as trapping and aerial delivery of oral toxicants, may also indirectly affect prey densities by temporarily suppressing BTS over larger areas (Engeman & Vice, 2001).

These swings in food availability allowed us to test whether the strength of selection on traits that influence AMS and ARS varied over time within the BTS study population. This question has important implications for control, in that strength of selection may influence the genetic diversity of the population (Colautti & Barrett, 2013), and thus the capacity of the population to respond when challenged by environmental change. The goals of this study were to: (1) Test for significant temporal variation in strength of selection on traits previously identified as important to AMS and ARS, (2) evaluate consequences of selection for the heterozygosity of offspring, and (3) interpret the manner by which changes in prey availability and offspring heterozygosity will impact future BTS control.

HYPOTHESES

We tested two central hypotheses. First, we posited that significant temporal variability existed in the strength of selection on predictors of AMS and ARS in both sexes (see **CHAPTER 1**). We specifically predicted that selection on age, trappability, and body condition as it relates to AMS in both sexes varied significantly over time. For males, significant variability was predicted for selection on age, AMS, and body condition as it related to ARS over time. For females, we predicted significant temporal variability in the effects of age, AMS, and degree of inbreeding as it related to female ARS. Environmental fluctuations, to include food availability, will impact relative fitness (Edeline et al., 2007), and this will cause trait selection to fluctuate significantly as a result. In our study species, prey availability can influence reproductive ecology by modifying hormone profiles, body condition, growth rate, movements, and recruitment (Christy et al., 2017; Moore et al., 2005; Waye & Mason, 2008). Therefore, each trait previously identified as important for AMS/ARS may also encounter selective pressures that will fluctuate in lockstep with prey abundance.

Second, we hypothesized that selection on traits that influence ARS also affects average genetic variability of offspring born that year. Specifically, we predicted that strength of selection on AMS would impact the multilocus heterozygosity of offspring (Coltman, Pilkington, Smith, & Pemberton, 1999). If individuals with multiple mating partners produce more offspring, then average genetic variability of offspring born in years of strong selection on mating success should exceed that for offspring born during years when selection on mating success is weaker. Previous studies in other organisms have demonstrated that females that mated with multiple males produced offspring with greater genetic variability (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; Yasui, 1998).

MATERIALS AND METHODS

Study Population—

The study site is a five ha experimental enclosure in northern Guam that was closed to immigration/emigration in 2004 (Rodda, Savidge, Tyrrell, Michelle, & Ellingson, 2007). In a previous study (**CHAPTER 1**), double-digest restriction site associated DNA sequencing (ddRAD) was employed to identify 6,180 single nucleotide polymorphisms (SNPs) present in >95% of the population. The most informative of these (N=654) were juxtaposed with sex and birth year to construct a multi-generational pedigree (N=426 individuals) with birth years extending from 2002-2016. We then estimated AMS and ARS for each individual, where AMS is defined as the total number of mates with which an individual produced offspring per annum, and ARS as the total number of offspring produced by an individual per annum.

Three primary results from our previous study were that: (1) AMS for each sex was significantly affected by age, body condition, and trappability, (2) ARS for males was significantly impacted by age, AMS, and body condition, and (3) female ARS was significantly affected by age, AMS, and degree of inbreeding (**CHAPTER 1**). This previous research on the study population employed 15 years of data (**CHAPTER 1**), whereas analyses herein utilized only those years (=9 years; APPENDIX FIGURES S1 – S4) in which known individuals were born and the parents of the individuals were measured during their birth year. This allowed relative variance in ARS to be derived for each year in which offspring were born.

Quantification of Selection Differentials and Gradients per Annum—

For each fitness trait above, we estimated annual standardized linear selection differentials and gradients (subsequently referred to as “differentials” and “gradients”). The differentials estimate the total strength of selection on a given trait, to include direct and indirect forms acting through correlated traits, whereas the gradients measure only direct selection (Kingsolver et al., 2001). These estimates required both fitness metrics and trait values to be standardized (Lande & Arnold, 1983), so as to facilitate comparisons among years (Kingsolver et al., 2001). Relative mating success was estimated per annum by dividing absolute AMS by mean sex-specific mating success, such that male AMS was relative to mean male AMS, with the same calculation for females. Relative reproductive success was also estimated in a similar manner for each sex. Trait-values were also standardized by year and sex (i.e., [illegible]=0, sd=1).

Differentials and gradients were estimated per annum and by sex, with individuals born during a calculated year being excluded so as to not confound parental and offspring fitness. This resulted in 77 records being excluded (out of 1,129, <7%). To estimate differentials for traits, relative annual fitness was regressed onto annual mean-standardized trait-values. Specifically, we performed simple linear regressions of sex-specific relative mating success versus mean-standardized age, body condition, and trappability per annum. Additionally, we performed simple linear regressions of male relative reproductive success versus mean-standardized age, annual mating success, and body condition per annum. The same was done for females, but employing mean-standardized age, annual mating success, and inbreeding per annum. The slope of relative fitness versus mean-standardized trait values equates to the annual standardized linear selection differential of the trait and represents the total strength of selection on a trait, to include direct and indirect forms acting through correlated traits (Hendry, 2017).

To estimate gradients per annum, multiple linear regressions were performed in which annual relative fitness was regressed onto all mean-standardized traits per sex. The partial regression coefficients equate to the annual standardized linear selection gradients of the traits (Lande & Arnold, 1983), or the strength of direct selection on the traits that year. All linear models were fit in *Rstudio* (*R v. 3.5.0*) with the *lm* function of the *R Stats* package (R Core Team, 2013).

Temporal Variation in Strength of and Opportunity for Selection—

After estimating differentials and gradients per annum, we tested whether selection on each trait varied over time by fitting sex-specific generalized linear mixed models (GLMMs), with trait-by-year interactions as random effects (Marrot, Charmantier, Blondel, & Garant, 2018). GLMMs were fit in *Rstudio* (*R v. 3.5.0*; RStudio Team, 2015) with the package *glmmTMB* (Brooks et al., 2017). All GLMMs employed a Poisson error distribution with a log-link, given that response variables (i.e., sex-specific AMS/ARS) are represented by count data (Zuur, Ieno, Walker, Savaliev, & Smith, 2009) with [illegible]<5 (DuVal, 2012). We validated the choice of this distribution for each model by testing for over-dispersion (all *P* >0.05) and by plotting scaled residuals against predicted values [simulated in *Rstudio* (*R v. 3.5.0*; RStudio Team, 2015) with the *DHARMa* package (Hartig, 2017)].

To test for significant temporal variation, we modeled fitness as a linear function of predictors previously identified as important to the fitness metric and individual and trait-by-year interactions as random effects. Individual was included as a random effect because individuals were sampled multiple times over years, and this dependency was accommodated so as to avoid pseudo-replication (Zuur, Ieno, & Elphick, 2010). Specifically, we tested for temporal variation in selection on each predictor of male AMS by modelling it as a linear function of fixed effects (i.e., age + body condition + trappability), and random effects (i.e., trait-by-year interactions + individual). Female AMS was similarly modelled, but with the inclusion of inbreeding coefficient as a fixed effect as it was present, though not significant, in the top model of female AMS in a previous study (**CHAPTER 1**).

To test for significant temporal variation in strength of selection on predictors of male ARS, male ARS was modelled as a linear function of age, AMS, and body condition (as fixed effects), with individual and trait-by-year interactions (as random effects). Trappability and level of inbreeding were also included as fixed effects as they were present, though not significantly so, in the top model of male ARS from our previous study. Similarly, to test for significant temporal variation in strength of selection on predictors of female ARS, it was modelled as a linear function of age, AMS, and degree of inbreeding (as fixed effects), with individual and trait-by-year interactions (as random effects). Body condition and trappability were also included as fixed effects as they were also present, again not significantly so, in the top model of female ARS identified from our previous study (**CHAPTER 1**).

Statistical significance of temporal variation in selection on each trait was gauged by comparing a global model with all fixed effects plus random effects of ID and trait-by-year interactions versus a model in which one trait-by-year interaction was excluded (Millet, Pelletier, Bélisle, & Garant, 2015). Likelihood ratio tests compared models with and without the trait-by-year random effect (Millet et al., 2015). If the log-likelihood of the model containing the trait-by-year interaction was significantly greater than the model lacking it, then the former was interpreted as having greater explanatory power, with significant temporal variability in strength of selection on the trait (Millet et al., 2015).

The opportunity for selection per annum is equal to the relative variance in reproductive success, and as such, establishes an upper limit on the strength of selection per annum (Arnold, 1986; Arnold & Wade, 1984). Thus, we calculated the annual opportunity for selection by sex as the variance in ARS divided by mean-squared ARS.

Temporal Variation in Cohort Heterozygosity—

We estimated mean observed heterozygosity of individuals born per annum. We had previously identified 6,180 SNPs present in >95% of the population (**CHAPTER 1**), and these were input into program *PLINK 1.9* (Purcell et al., 2007) to test for and discard loci displaying significant linkage disequilibrium (LD) and departures from Hardy-Weinberg Equilibrium (HWE). All individuals born from 2002-2004 (i.e., when the population was experimentally closed) were considered as founders (n=24).

We tested for LD with the *--indep* function, evaluating 50 SNP windows sliding 5 at a time, and with a variance inflation factor (VIF)=2. A minor allele frequency (MAF) cut-off was not established because we wished to maximize the number of loci (and proportion of the genome) analyzed. The pruned data set of 1,060 SNPs was imported into *Rstudio* (*R v. 3.5.0*; RStudio Team, 2015) where we calculated standardized multilocus heterozygosity (sMLH; Coltman et al., 1999) using the package *inbreedR* (Stoffel et al., 2016). Individual sMLH was calculated as %-heterozygous loci divided by mean heterozygosity. By so doing, individual multilocus heterozygosity could be calculated even when all individuals were not typed at the same loci (Coltman et al., 1999). We then estimated mean and variance of sMLH for individuals born per annum.

We wished to determine if the genetic variability of the resulting cohort was related to temporal variation in selection on traits directly related to ARS. Specifically, we focused on sex-specific AMS as only this trait exhibited significant temporal variation in selection (see results). To accomplish this, we constructed a linear model in which mean cohort sMLH was the response variable, and gradients in female AMS were predictors. Only female AMS was used as there was high collinearity between male and female AMS gradients (VIF>2). It should be noted, however, that while male AMS gradients were removed from the model, they may still potentially drive model results, rather than (or in addition to) female AMS gradients (Zuur et al., 2010). We fit the linear model in *Rstudio* (*R v. 3.5.0*; RStudio Team, 2015) with the *lm* function of the *R Stats* package (R Core Team, 2013).

RESULTS

Temporal Variability in Selection—

We found significant temporal variability in the effect of age on sex-specific AMS (likelihood ratio tests, $P<0.001$). Male selection gradients (β) for age were significant with regards to relative mating success for 2010 ($\beta=0.749\pm0.311$, $P=0.018$) and 2013 ($\beta=0.773\pm0.303$, $P=0.019$). In essence, older males produced offspring with significantly more females than younger males during these years. Similarly, selection gradients of female age with regards to relative mating success were significantly positive for years 2009 ($\beta=0.367\pm0.177$, $P=0.042$) and 2010 ($\beta=0.997\pm0.257$, $P< 0.001$), such that older females produced offspring with relatively more males than did younger females. Interestingly, these three years (i.e., 2009, 2010, 2013) were associated with (or subsequent to) elevated food availability for adults (Reed et al., unpublished data; Yackel Adams et al., unpublished data). Temporal variation in the effects of trappability and body condition on sex-specific AMS were non-significant (likelihood ratio tests; all $P>0.05$). Yet, statistically significant gradients for body condition were associated in both sexes with years of elevated food availability, or directly following high-prey years (e.g., 2010; Appendix Table S1).

We only identified significant temporal variability in the effects of AMS on sex-specific ARS (likelihood ratio tests; both $P<0.001$). Differentials (S=total selection) and gradients (β=direct selection only) were significant for AMS in both sexes across all years (Table 1). Yet, strength of selection fluctuated yearly (likelihood ratio tests, $P<0.05$), with lowest values in years associated with (or subsequent to) high food availability. Lowest values for direct selection on female mating success corresponded to the year (and subsequent year) of a food supplementation experiment [i.e., 2009–2010 (Reed et al., unpublished data)], as well as years of high rodent density (i.e., 2012–2013) that followed removal of adults and sub-adults (mid-2011; Yackel Adams et al., unpublished data). This trend was also apparent for males, save for differentials and gradients in 2012.

We did not find significant temporal variability in the strength of selection on sex-specific age, male body condition, or female inbreeding with respect to sex-specific ARS (TABLE 1). Yet, significant differentials [i.e., total selection (direct + indirect)] were observed for sex-specific age and male body condition that generally corresponded to years of high food availability (TABLE 2). For example, significant selection on male body condition (or unmeasured traits affecting male body condition) only occurred in years associated with (or subsequent to) high prey abundance (2009–2010, 2012–2013). Therefore, during years when food availability was elevated, older individuals of both sexes and those males with better body condition produced relatively more offspring than did younger individuals or males with poor body condition.

Opportunities for Annual Selection and Temporal Variation in Mean Cohort sMLH—

The female opportunity for selection, or relative variance in female reproductive success, ranged from 1.04 (2013) to 100.00 (2011; TABLE 3). For males, values ranged from 3.91 (2013) to 107.00 (2011). In general, relative variance in reproductive success was lowest in years when differentials for age (both sexes) and body condition (males only) were significant, and when selection on male and female AMS was weakest. Relative variance in reproductive success was greatest in years when gradients for AMS were largest (both sexes).

Individuals born during the nine years of this study had mean sMLH=0.989 (±0.113). Average cohort sMLH ranged from 0.966 (±0.088) in 2009 to 1.059 (±0.048) in 2011 (APPENDIX TABLE S2). There was a significant relationship between the magnitude of selection on female AMS and the mean heterozygosity of offspring born during the year of selection (FIGURE 1; r^2=0.488, P<0.036).

DISCUSSION

Overview—

The prevalence of temporal variability in selection among wild populations has recently gained significant attention (Siepielski et al., 2009), yet few studies have established a link between it and environmental conditions (Siepielski, DiBattista, Evans, & Carlson, 2011). When such studies are attempted, there is a tendency to focus solely on large-scale climatic aspects [e.g., precipitation, Siepielski et al. (2017); temperature, Visser et al., (2015)]. Yet, effective management of invasive species, for example, requires an understanding of how control measures influence selection, often on a more local and/or regional scale.

Here, we identified significant temporal variability in strength of selection that coincides with control measures used to manage an invasive species. Further, we found a significant relationship between the annual strength of selection on female AMS and the genetic variability of offspring. This, in turn, highlights the importance of quantifying temporal aspects of selection as a potential means of controlling the genetic variability of the target species. The relationship between strength of selection and offspring genetic variability is particularly prudent for invasive species, in that founder effects most often hold sway in these situations. Thus, strength of selection provides a potential mechanism to modulate genetic variability, and thus evolvability, despite rigorous control. These approaches therefore allowed us to explore the consequences of management in an invasive population, particularly with regard to the strength of selection and the evolutionary trajectory that results.

Temporal Variability in Strength of Selection—

We found significant temporal variability in the effects of age on AMS in both male and female BTS, with significant selection gradients for age corresponding with three years associated with (or subsequent to) high adult prey availability (i.e., females: 2009, 2010; males: 2010, 2013). Therefore, older individuals produced offspring with a significantly greater number of mates in these years than did younger individuals. It is not particularly surprising that older individuals would have a mating advantage during years (or subsequent years) of high prey availability. An abundance of prey allows those older and larger to maintain body size (Moore et al., 2005; Waye & Mason, 2008). Further, adequate food resources to support large body sizes also reduces stress that acts to suppress reproduction (Aldridge, Siegel, Bufalino, Wisniewski, & Jellen, 2010; Moore et al., 2005).

We also found significant temporal variation in the effects of AMS on ARS for both sexes. Statistically significant gradients for AMS were apparent in both sexes per annum as well. In general, selection was strongest during years of low prey availability and weakest during high prey availability. To illustrate, the weakest gradients occurred for each sex in 2009, 2010, and 2013, with female gradients also weakest in 2012 (TABLE 1). In 2009, a food supplementation experiment occurred (Reed et al., unpublished data), with ample prey abundance in 2009. Similarly, all adults and sub-adults were removed in mid-2011 (Yackel Adams et al., unpublished data), and this also promoted an abundance of prey in 2012 and 2013.

Our results are intuitive in the context of opportunities for selection, or sex-specific relative variance in reproductive success. First, individuals are capable of acquiring enough energy to reproduce when prey is abundant (Waye & Mason, 2008). Furthermore, food availability reduces stress that inhibits reproduction, such that more individuals are sexually active when food is plentiful (Aldridge et al., 2010; Moore et al., 2005). Competition for mates is affected by the operational sex ratio (OSR), a measure of the relative numbers of sexually active males and females in the population (Janicke & Morrow, 2018), and is consequently influenced by food availability (Aldridge et al., 2010; Moore et al., 2005; Waye & Mason, 2008). Therefore, food availability has an impact on the relative numbers of males and females available for mating, and as such, reduces competition for breeding success (Kvarnemo & Ahnesjo, 1996).

Furthermore, BTS move less and have smaller activity areas when prey is abundant (Christy et al., 2017), and this may also serve to decrease encounters among individuals (Shine, 2003). If a greater number of adults are reproducing, and they move less and encounter fewer mates, then relative variance in reproductive success (i.e., opportunity for selection) will decline. The opportunity for selection limits the strength of directional selection on a trait (Arnold & Wade, 1984), with lower AMS gradients resulting. Indeed, strength of selection on AMS has been shown to be weaker under benign conditions (i.e., high food availability) as compared to more stressful conditions in other systems [i.e., low food availability; Janicke, David, & Chapuis (2015)]. When food availability is low, BTS display larger activity areas and greater movement rates, with those in better condition moving farther and longer (Christy et al., 2017). This, in turn, promotes the likelihood of encountering multiple mates (Shine, 2003). When these data are combined with physiological responses to food stress (Buchanan, 2000), and effects of food availability on numbers of sexually active individuals (Janicke et al., 2015), a large variance in reproductive success would be expected, with some individuals subsequently acquiring multiple mates and producing more offspring.

Effects of food availability on OSR and mate competition have been specifically identified in other organisms (Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjo, 1996), with impacts varying by sex (Gwynne & Simmons, 1990). Furthermore, individuals may also vary in their physiological response to stress (Buchanan, 2000), such that some reflect a greater mating advantage during times of low food availability [e.g., BTS with better body condition move more often and have larger activity areas (Christy et al., 2017), thus potentially encountering more mates]. Yet, the manner by which food availability impacts competition or mate encounters in BTS is still unknown. Therefore, we anticipate future work that will characterize the mechanisms by which high food availability promotes weaker selection on AMS.

Selection and its Impact on Genetic Variability of Offspring—

Importantly, we found female AMS had a significant impact on the average sMLH of offspring born during the year of selection. However, it is also possible that the gradient for male (rather than female) AMS was driving this relationship, due to collinearity between the two (Zuur et al., 2010). Despite this, we assume the female selection gradient for AMS influenced the heterozygosity of offspring, as multiple mating by females is known to impact offspring genetic variability (Foerster et al., 2003).

Multiple paternity (i.e., the phenomenon in which a single clutch is fertilized by multiple males) is common in snakes (Uller & Olsson, 2008) and has been confirmed for BTS through genetic pedigree reconstruction (Lardner et al., in prep). One hypothesis for multiple paternity is the positive effect it has on offspring heterozygosity (Foerster et al., 2003). If multiple males sire a single clutch, then more alleles are represented, and average heterozygosity will be greater than if all were sired by the same male. In addition, numerous studies have validated the relationship between individual heterozygosity and fitness (Chapman, Nakagawa, Coltman, Slate, & Sheldon, 2009). Therefore, the fitness of offspring can be promoted through multiple mating. Our results indicate that when selection on mating success is strong such that females acquire more mates and produce more offspring, then those offspring will have greater heterozygosity and (we intuit) fitness as well.

Implications for Brown Treesnake Control—

Temporal variation in the strength of selection on female AMS coincides with prey availability, and also the genetic variability of offspring birthed that year. Additionally, a potential tool for BTS control on Guam is prey suppression (Christy et al., 2017), and low prey availability has been offered as evidence for a concomitant decline in BTS abundance (Moore et al., 2005). Indeed, a decline in prey depresses recruitment (Yackel Adams et al., unpublished data), yet it also drives the strength of selection on female AMS such that some individuals acquire multiple mates and produce more offspring. Unfortunately, this also yields greater heterozygosity in offspring. Therefore, while prey suppression and natural prey declines appear promising for BTS control, they may also promote genetic variability and facilitate an adaptive response to environmental change.

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APPENDIX

Figures and Tables—

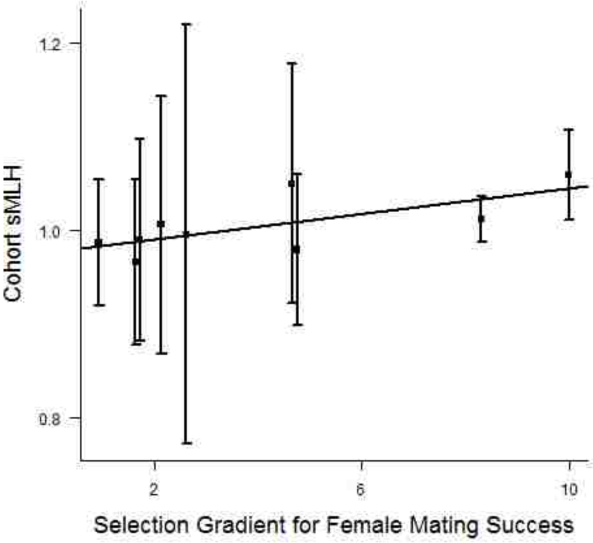

FIGURE 1. Standardized multilocus heterozygosity (sMLH) estimated for Brown Treesnake (*Boiga irregularis*) from an experimentally-closed population on Guam. Average sMLH was calculated for individuals born during the same year (N=9 cohorts) and regressed on to annual standardized linear selection gradients of female mating success for each year. The relationship between cohort sMLH and the selection gradient for female mating success was significant (slope coefficient=0.007; r^2=0.49; P<0.035). Data points are shown ±1 standard deviation.

TABLE 1. Annual standardized linear selection gradients (*β*) for predictors of annual reproductive success in (A) male and (B) female Brown Treesnake (*Boiga irregularis*) from an experimentally-closed population on Guam. Annual selection gradients represent the strength of direct linear selection acting on the trait during the year. Significant *P*-values are in bold. SE=standard error.

(A)

Males										
		Mating Success			Age			Body Condition		
Year	N	*β*	SE	*P*	*β*	SE	*P*	*β*	SE	*P*
2007	43	3.695	0.000	**<0.001**	0.000	0.000	0.331	0.000	0.000	0.623
2008	39	2.805	0.000	**<0.001**	0.000	0.000	0.203	0.000	0.000	0.823
2009	58	1.911	0.071	**<0.001**	-0.010	0.067	0.888	0.051	0.071	0.473
2010	93	2.719	0.076	**<0.001**	-0.086	0.084	0.306	0.061	0.084	0.470
2011	107	10.340	0.000	**<0.001**	0.000	0.000	0.693	0.000	0.000	0.744
2012	36	3.425	0.130	**<0.001**	0.158	0.125	0.216	-0.079	0.140	0.575
2013	24	1.918	0.101	**<0.001**	-0.035	0.076	0.651	0.072	0.094	0.451
2015	53	7.280	0.000	**<0.001**	0.000	0.000	0.378	0.000	0.000	0.308
2016	44	2.855	0.203	**<0.001**	0.088	0.203	0.666	0.014	0.205	0.945

(B)

Females							
		Mating Success			Age		
Year	N	*β*	SE	*P*	*β*	SE	*P*
2007	45	4.642	0.165	**<0.001**	0.105	0.165	0.531
2008	44	4.626	0.149	**<0.001**	0.085	0.149	0.572
2009	68	1.632	0.084	**<0.001**	-0.044	0.084	0.600
2010	100	2.128	0.107	**<0.001**	0.089	0.107	0.409
2011	100	10.000	0.000	**<0.001**	0.000	0.000	0.557
2012	38	1.715	0.259	**<0.001**	0.068	0.259	0.793
2013	27	0.925	0.080	**<0.001**	0.074	0.080	0.364
2015	69	8.307	0.000	**<0.001**	0.000	0.000	0.207
2016	64	2.612	0.192	**<0.001**	-0.157	0.192	0.415

TABLE 2. Annual standardized linear selection differentials (*S*) for predictors of annual reproductive success in (A) male and (B) female Brown Treesnake (*Boiga irregularis*) from an experimentally-closed population on Guam. Annual selection differentials represent the strength of total linear selection acting on the trait during the year, including direct selection acting on the trait and indirect selection acting on correlated traits. Significant *P*-values are in bold. SE=standard error.

(A)

Males

		Mating Success			Age			Body Condition		
Year	N	*S*	SE	*P*	*S*	SE	*P*	*S*	SE	*P*
2007	43	3.695	0.000	**<0.001**	1.478	0.529	**0.008**	-0.296	0.575	0.610
2008	39	2.805	0.000	**<0.001**	0.419	0.456	0.364	-0.234	0.460	0.614
2009	58	1.929	0.066	**<0.001**	-0.056	0.266	0.833	0.705	0.249	**0.006**
2010	93	2.709	0.068	**<0.001**	0.969	0.274	**0.001**	1.037	0.271	**0.000**
2011	107	10.340	0.000	**<0.001**	-0.266	1.009	0.792	0.638	1.008	0.528
2012	36	3.432	0.109	**<0.001**	1.173	0.564	**0.045**	1.797	0.513	**0.001**
2013	24	1.952	0.067	**<0.001**	0.721	0.393	0.080	1.346	0.309	**0.000**
2015	53	7.280	0.000	**<0.001**	0.157	1.019	0.878	-0.385	1.018	0.707
2016	44	2.862	0.195	**<0.001**	0.374	0.479	0.440	-0.513	0.476	0.288

(B)

Females

		Mating Success			Age		
Year	N	*S*	SE	*P*	*S*	SE	*P*
2007	45	4.689	0.146	**<0.001**	2.213	0.647	**0.001**
2008	44	4.636	0.146	**<0.001**	0.597	0.724	0.415
2009	68	1.619	0.080	**<0.001**	0.435	0.208	**0.040**
2010	100	2.168	0.096	**<0.001**	1.039	0.215	**0.000**
2011	100	10.000	0.000	**<0.001**	-0.468	1.009	0.644
2012	38	1.748	0.225	**<0.001**	0.886	0.337	**0.012**
2013	27	0.951	0.074	**<0.001**	0.404	0.188	**0.041**
2015	69	8.307	0.000	**<0.001**	-0.206	1.015	0.840
2016	64	2.590	0.190	**<0.001**	0.206	0.379	0.589

Table 3. Opportunities for selection were calculated for (A) male and (B) female Brown Treesnake (*Boiga irregularis*) in an experimentally-closed population in Guam. For each year of nine years, opportunity for selection was calculated as the sex-specific variance in reproductive success divided by the squared mean of sex-specific reproductive success. The annual opportunity for selection sets an upper on the annual strength of directional selection and is equal to the annual sex-specific relative variance in reproductive success.

(A)

	Year								
	2007	2008	2009	2010	2011	2012	2013	2015	2016
Sample Size	43	39	58	93	107	36	24	53	44
Mean	0.07	0.15	1.28	0.63	0.01	1.39	1.25	0.02	0.23
Variance	0.07	0.19	6.45	3.13	0.01	23.50	6.11	0.02	0.51
Opportunity for Selection	13.65	7.87	3.96	7.77	107.00	12.18	3.91	53.00	9.78

(B)

	Year								
	2007	2008	2009	2010	2011	2012	2013	2015	2016
Sample Size	45	44	68	100	100	38	27	69	64
Mean	0.11	0.11	0.66	0.43	0.01	0.79	1.19	0.01	0.22
Variance	0.28	0.29	1.33	1.04	0.01	3.04	1.46	0.01	0.43
Opportunity for Selection	22.91	22.39	3.04	5.60	100.00	4.87	1.04	69.00	8.94

Supplemental Figures and Tables—

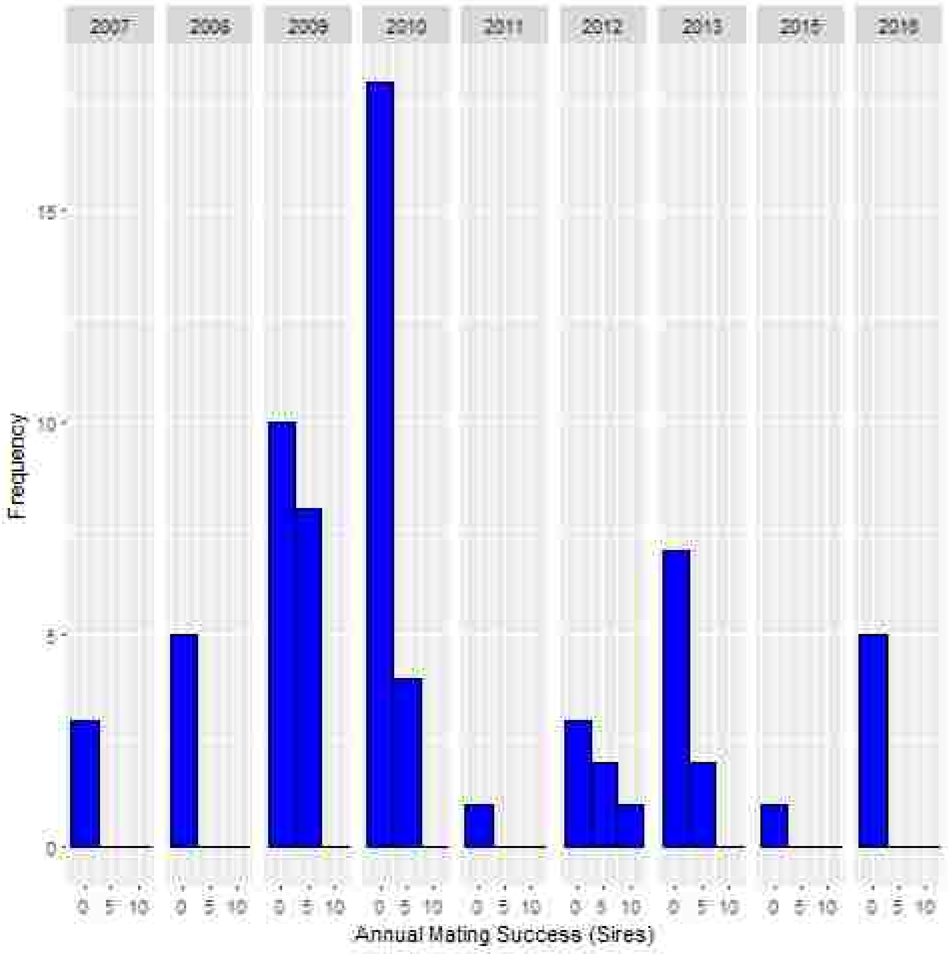

FIGURE S1. Histogram of annual mating success (= number of mating partners with which an individual produced offspring during a year) of male Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

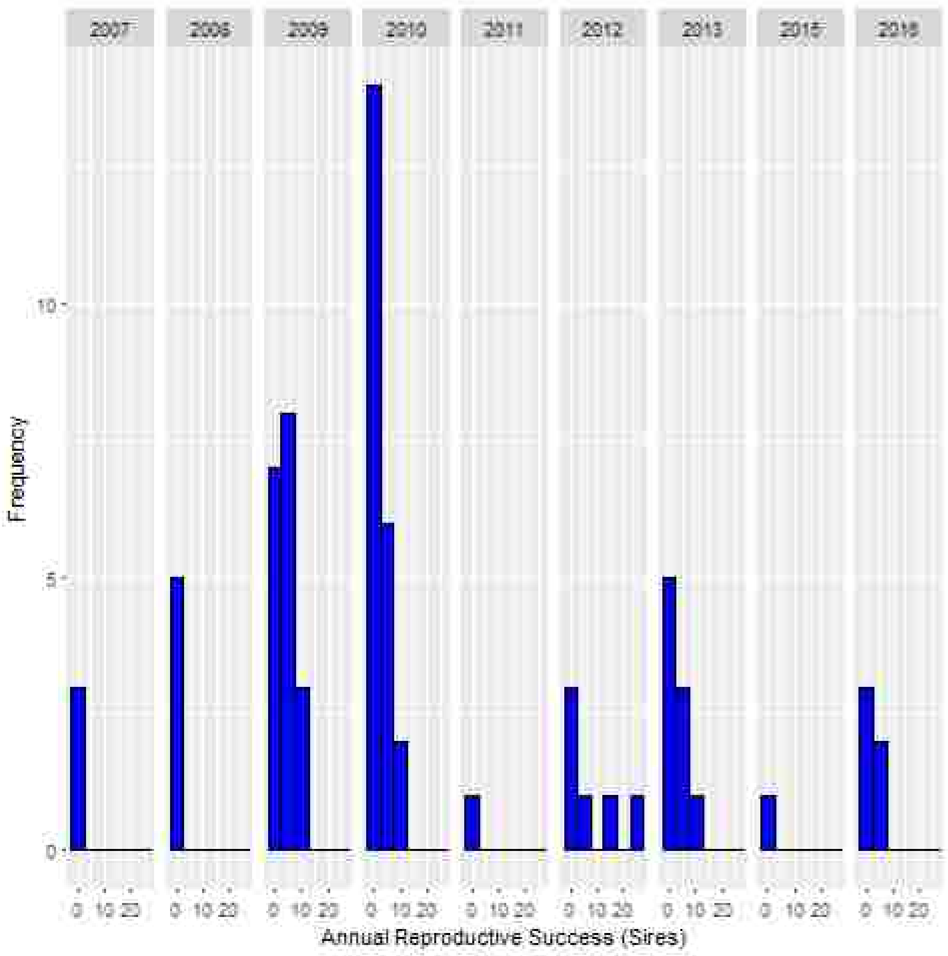

FIGURE S2. Histogram of annual reproductive success (= number of offspring sired an individual during a year) for male Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual reproductive success > 0 are shown.

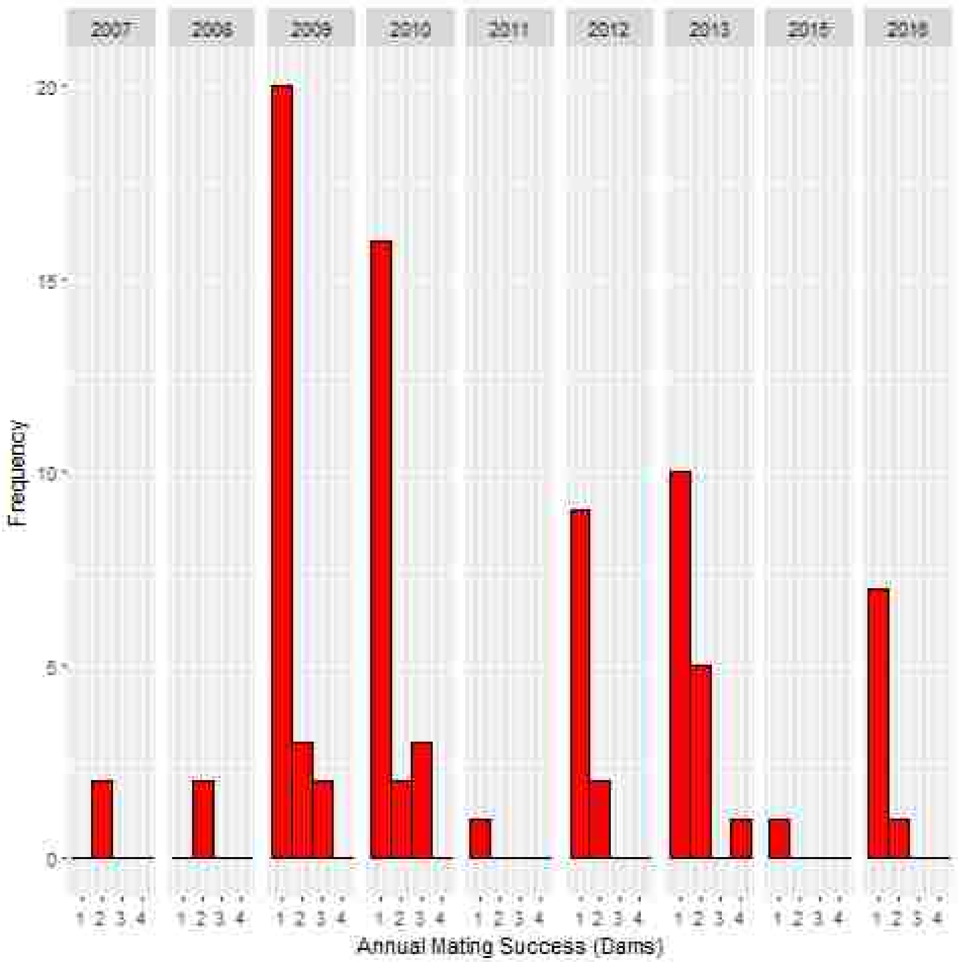

FIGURE S3. Histogram of annual mating success (= number of mating partners with which an individual produced offspring during a year) of female Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual mating success > 0 are shown.

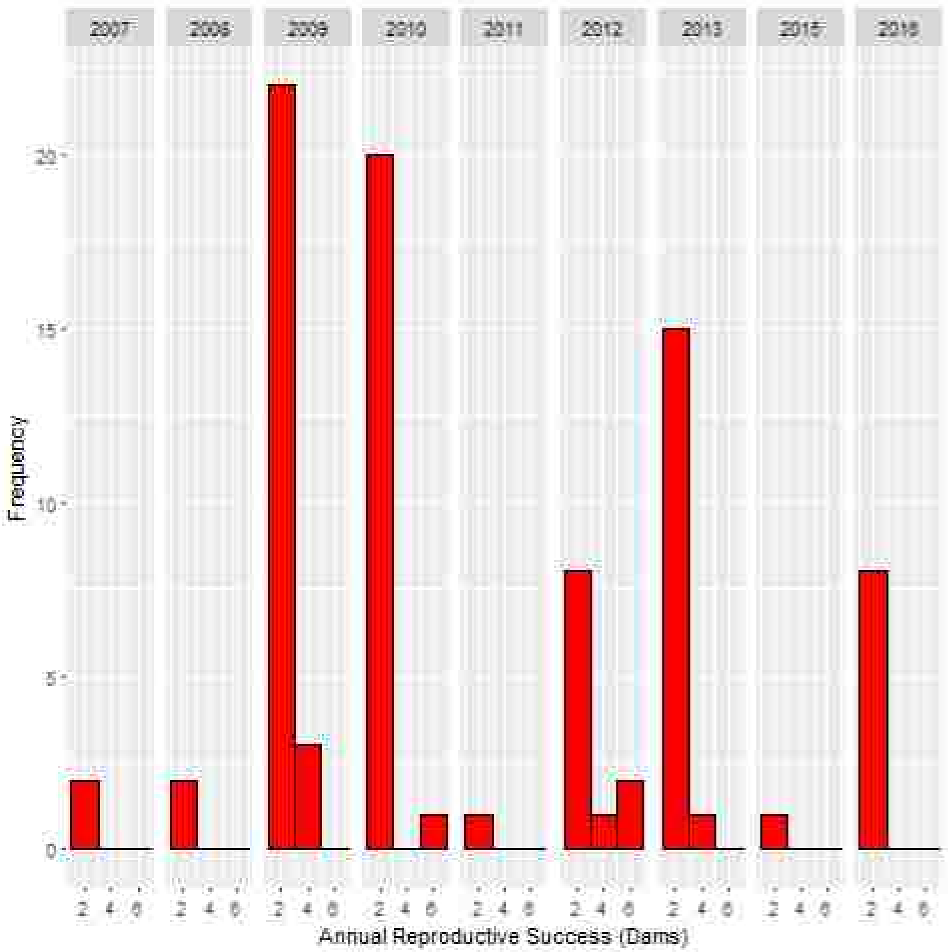

FIGURE S4. Histogram of annual reproductive success (= number of offspring sired an individual during a year) for female Brown Treesnake (*Boiga irregularis*) from an experimentally closed population on Guam. Only data for individuals with annual reproductive success > 0 are shown.

TABLE S1. Annual standardized linear selection gradients (β) for predictors of annual mating success in (A) male and (B) female Brown Treesnake (*Boiga irregularis*) on Guam. Annual selection gradients represent the strength of direct linear selection acting on the trait during the year. Significant *P* values are in bold. SE=standard error.

(A)

		Body Condition			Trappability			Age		
Year	N	β	SE	*P*	β	SE	*P*	β	SE	*P*
2007	43	-0.186	0.427	0.665	2.903	0.540	**0.000**	-0.435	0.556	0.438
2008	39	-0.021	0.489	0.967	0.544	0.493	0.277	0.248	0.495	0.620
2009	58	0.507	0.266	0.062	0.331	0.265	0.216	-0.097	0.238	0.685
2010	93	0.576	0.285	**0.046**	-0.290	0.264	0.274	0.749	0.311	**0.018**
2011	107	0.638	1.037	0.540	0.255	1.179	0.829	-0.293	1.174	0.803
2012	36	1.571	0.549	**0.007**	0.064	0.484	0.895	0.247	0.547	0.654
2013	24	0.980	0.286	**0.003**	-0.461	0.313	0.157	0.773	0.303	**0.019**
2015	53	-0.317	1.078	0.770	-0.451	1.217	0.713	0.416	1.181	0.726
2016	44	-0.824	0.506	0.111	-0.835	0.535	0.126	0.461	0.488	0.351

(B)

		Body Condition			Trappability			Age		
Year	N	β	SE	*P*	β	SE	*P*	β	SE	*P*
2007	45	-0.267	0.658	0.688	1.087	0.815	0.190	1.416	0.803	0.085
2008	44	0.857	0.754	0.262	0.118	0.764	0.878	0.668	0.754	0.381
2009	68	0.422	0.179	**0.021**	0.164	0.181	0.368	0.367	0.177	**0.042**
2010	100	0.085	0.255	0.741	-0.191	0.210	0.363	0.997	0.257	**0.000**
2011	100	0.577	1.039	0.580	-0.422	1.261	0.739	-0.332	1.269	0.794
2012	38	0.918	0.249	**0.001**	0.129	0.224	0.568	0.335	0.256	0.200
2013	27	-0.038	0.228	0.870	-0.136	0.215	0.532	0.429	0.231	0.076
2015	69	1.724	1.016	0.095	-0.658	1.193	0.584	0.367	1.203	0.761
2016	64	-0.175	0.352	0.620	0.813	0.349	**0.023**	0.178	0.358	0.621

TABLE S2. Standardized multilocus heterozygosity (sMLH) was estimated for individual Brown Treesnake (*Boiga irregularis*) born during each of the nine years in this study (= ‘Cohort’). Mean sMLH and standard deviation (SD) are presented for each cohort. N=number of individuals per cohort.

Cohort	N	sMLH	SD
2007	17	1.050	0.128
2008	14	0.979	0.080
2009	100	0.966	0.088
2010	64	1.006	0.138
2011	3	1.059	0.048
2012	53	0.990	0.108
2013	41	0.986	0.067
2015	4	1.011	0.025
2016	15	0.995	0.224

Chapter 3: Heritability of Traits Important for Annual Reproductive Success in the Highly Invasive Brown Treesnake (*Boiga irregularis*) on Guam

ABSTRACT

Unanticipated results can often occur when specific traits of an invasive species are preemptively targeted by control methods. This is because the underlying additive genetic variation of the trait is targeted as well, and given this, effects can instead be cued that are different from those originally targeted. If, for example, the trait is tied to reproductive success, then selection can promote *sensu lato* the vital rates of the population under control. We tested this hypothesis by evaluating traits related to annual mating and reproductive success [i.e., trappabillty, body condition, snout-vent length (=SVL)] to determine the potential for an adaptive response to selection, as imposed by control of invasive Brown Treesnake (*Boiga irregularis,* BTS). To do so, we used "animal models" as implemented with *MCMCglmm* to estimate repeatability (*R*), additive genetic variance (V_A), and narrow-sense heritability (h^2) of these four traits, as gauged within an experimentally-closed population established on northern Guam (N=426) in 2004. We found low but significant h^2 for annual trappability (h^2=0.050), and body condition (h^2=0.035), whereas SVL and annual mating success lacked significant additive genetic variation. However, annual mating success was significantly repeatable (*R*=0.589), underscoring its iterative capacity year-to-year. We found that adaptive evolution of traits related to trappability and body condition were possible in response to selection imposed by control methods, and these results highlight the repercussions that can stem from active management, particularly as it relates to average annual reproductive success in our BTS population.

INTRODUCTION

Artificial Selection and Adaptive Evolution—

Artificial selection has long been used as a mechanism to promote desirable traits in animals and plants [reviewed in Hill & Caballero (1992)]. Yet, the same principle that facilitates an adaptive response to breeding pressures [i.e., breeder's equation (Lush, 1937)] allows unintentional adaptive evolution to be promoted as well (Allendorf & Hard, 2009). Human-induced adaptive evolution is possible with any form of artificial selection, provided the phenotypic target of selection is correlated with relative fitness, and governed at least in part by additive genetic variation (Waples & Naish, 2009).

Artificial selection is also of concern for conservation and management of natural populations, as the strength of selection imposed by hunting or fishing can outpace that of natural selection (Darimont et al., 2009). For instance, the collapse of the Atlantic cod fishery in the late 20th century is attributed to heavy fishing pressure that, in addition to reducing population size, also drove the evolution of earlier sexual maturity and lower reproductive rates (Olsen et al., 2004). Similarly, pressure imposed by trophy hunting also elicits the evolution of less 'showy' phenotypes as well as smaller adult body sizes (e.g., Fenberg & Roy, 2008; Chiyo, Obanda, & Korir, 2015; Pigeon, Festa-Bianchet, Coltman, & Pelletier, 2016). Both examples emphasize the magnitude of evolutionary change that can result over ecologically-relevant time scales when strong directional selection is imposed on traits that maintain additive genetic variation.

On the other side of the conservation "coin," artificial selection is also an issue with regard to control of invasive species (Závorka et al., 2018). Those methods that target specific traits of an invasive can also shift selection gradients to favor those not targeted by control. In this sense, if the traits are governed by underlying additive genetic variation, selection can promote their evolution such that the population becomes less amenable to control over time, thus thwarting adaptive management (e.g., Wendling & Wegner, 2015).

An additional consideration is that traits related to or influenced by control can also impact the average reproductive fitness in a population. If additive genetic variation underlies a trait related to that being controlled, and if the trait is also related to mating or reproductive success, then selection on the trait can also serve to influence the population birth rate. For example, invasive mosquitofish with shy personality phenotypes (i.e., less willing to engage in risk-taking behavior) are less trappable but also reflect the greatest reproductive success (Wilson, Godin, & Ward, 2010). If personality has additive genetic variation, selection by trapping over time may result not only in a mosquitofish population that is less trappable, but also with greater average reproductive success. These results, despite positive attempts at control, are contrary to the goals of invasive species management. This highlights the importance of balancing invasive species control with its consequences in light of ecological and evolutionary ('eco-evo') dynamics.

Brown Treesnake Control and its Evolutionary Consequences—

The highly invasive Brown Treesnake (*Boiga irregularis*; BTS) was introduced to the United States territory of Guam in a single, small event following World War II (Richmond, Wood, Stanford, & Fisher, 2014). Yet, by the 1980s, BTS had grown to a remarkable density of 100 snakes per hectare (Rodda & Savidge, 2007). Its presence on Guam has promoted a series of dramatic and cascading ecological changes, with primary focus on the devastation of endemic avifauna (e.g., Savidge, 1987; Mortensen, Dupont, & Olesen, 2008; Rogers, Hille Ris Lambers, Miller, & Tewksbury, 2012; Caves, Jennings, Hille Ris Lambers, Tewksbury, & Rogers, 2013). A series of economic and human health threats have also emerged (Perry & Vice, 2009).

A variety of control efforts have been implemented to reduce or eliminate BTS from Guam. Yet, these can potentially promote adaptive evolution by selecting against subsets of phenotypes in the population. For example, traps are often used as a control mechanism, but are biased with regard to snout-vent lengths (SVLs), and thus age classes, with longer/older

BTS being trapped more often (Rodda, Savidge, Tyrrell, Michelle, & Ellingson, 2007; Tyrrell et al., 2009). Furthermore, bolder individuals, or those more willing to engage in risk-taking behaviors (Wilson, Clark, Coleman, & Dearstyne, 1994), may be more likely to enter traps (i.e., greater trappability; Le Cœur et al., 2015), resulting in more shy individuals being selected for during bouts of heavy trapping (e.g., Wilson et al., 2010).

Control methods can also indirectly affect selection on BTS phenotypes. For example, a variety of control methods can elicit change in prey availability, to include active manipulation of prey abundance (Christy, Savidge, Yackel Adams, Gragg, & Rodda, 2017; Reed et al., unpublished data), and intense trapping of BTS (Yackel Adams et al., unpublished data). When control methods promote elevated prey availability, the result is a significant positive selection on body condition and age (and, by consequence, SVL). Similarly, the strength of selection on annual mating success (i.e., the number of individuals with which an individual produces offspring) also decreases across both sexes (**CHAPTER 2**).

Importantly, all four traits [i.e., (1) body condition, (2) trappability, (3) age, and (4) mating success] directly or indirectly (via effects on annual mating success) impact annual reproductive success of BTS (i.e., the number of offspring produced by an individual during a year; **CHAPTER 1**). Therefore, control methods have the capacity to impact not only the distribution of trait values in a population, but also the average annual reproductive success of individuals. If these traits have additive genetic variation, then control methods may promote adaptive evolution of these traits, and by consequence, affect average annual reproductive success, a result which may be diametrically opposed to management goals.

The purpose of this study was to test whether traits associated with mating and reproductive success in BTS have the capacity to adapt in response to selection via control measures. To do so, we first asked if the traits demonstrated repeatability [i.e., that proportion of total phenotypic variance in a population that represents consistent, reiterative differences among individuals (Falconer & Mackay, 1996)]. This measure is often, though not always, considered as an upper limit for the narrow-sense heritability of a trait (Dohm, 2002). Next, we partitioned individual trait variation into additive genetic versus permanent environment effects [e.g., maternal effects, common environment effects (Wilson et al., 2010)]. This allowed us to gauge if traits may undergo adaptive evolution in response to control by estimating their narrow-sense heritability [i.e., that proportion of total phenotypic variance due to additive genetic variance (Hoffmann & Merilä, 1999)].

HYPOTHESES

We hypothesized that four traits important for annual mating and/or reproductive success, and affected by control-related selection, would demonstrate significant heritability. These were: (1) body condition [i.e., residual of log-transformed mass on to log-transformed SVL (Schulte-Hostedde, Zinner, Mllar, & Hickling, 2005)], (2) trappability [i.e., number of times an individual was captured in a baited trap during a year (Le Cœur et al., 2015)], (3) SVL [used to extrapolate hatch date and estimate age (Lardner et al., in prep)], and (4) annual mating success (i.e., number of mates with which an individual produces offspring during a year). Each has shown significant additive genetic variation when gauged in other systems [e.g., body condition (Merilä, Kruuk, & Sheldon, 2001; Réale, Festa-Bianchet, & Jorgenson, 1999); trappability (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007), body size (Kruuk, 2017), mating success (Greenway & Shuker, 2015)].

MATERIALS AND METHODS

Study Site and Pedigree Reconstruction—

In 2009, we initiated DNA sampling of a BTS population located in a five ha^2 experimental enclosure on northern Guam that was closed to immigration and emigration in 2004 (Rodda et al., 2007). Extrapolated hatch dates for sampled individuals ranged from 2002 to 2016 (**CHAPTER 1**; Lardner et al., in prep). Previously, individuals in the study population (N=426) were genotyped at 654 single nucleotide polymorphisms (SNPs) derived from double-digest restriction site associated DNA (ddRAD) library preparation. The *R* package *Sequoia* (Huisman, 2017) was employed to reconstruct a 15-year pedigree from these data (**CHAPTER 1**), with 69 known females assigned as dams of 199 individuals, and 51 known males as sires of 257 individuals [APPENDIX FIGURE S1(A)]. *Sequoia* also assigned 47 dummy dams and 26 dummy sires to the pedigree as links among generations when groups of half-siblings did not have a sampled parent [Huisman, 2017; APPENDIX FIGURE S1(B)]. All individuals without a sampled or dummy parent were necessarily assumed to be unrelated to all other individuals in the study population (Wilson et al., 2010).

Animal Models—

We used “animal models” (Lynch & Walsh, 1998) to estimate the repeatability (*R*) and narrow-sense heritability (h^2) of traits important to BTS mating and/or reproductive success. The animal model is a special (generalized) linear mixed effects model that includes the additive genetic value of an individual as a random effect (Kruuk, 2004). The reasoning for this is that the precise additive genetic value of a trait for an individual is unknown (Wilson et al., 2010). Given this, an animal model allows for the estimation of variance in additive genetic values by comparing trait values of individuals with known degrees of relatedness. This, in turn, facilitates the partitioning of phenotypic variance into that due to an additive genetic versus 'other' effects (e.g., permanent environment effect, residual effect). Furthermore, because individuals share genes, additive genetic values fitted as a random effect also account for the non-independence of genes among individuals (Wilson et al., 2010).

We used the *R* package *MCMCglmm* (Hadfield, 2010) to construct our animal models because it accommodates non-Gaussian error distributions such as the Poisson necessary for modelling count data, as represented by annual trappability and mating success (Zuur, Ieno, Walker, Savaliev, & Smith, 2009). To gauge the presence of consistent, repeatable differences among individuals, we first partitioned the total phenotypic variance of each trait (V_P) into that between-individual (V_I) versus that residual (V_R). Additionally, we further partitioned V_I to separate out the contribution of additive genetic variance (V_A) to $V_{I.}$ After so doing, V_I (individual variance due to a permanent environment effect) can be considered as an extreme case of a common environment effect, due to factors such as maternal environment and maternal genetic effects, among others (Wilson et al., 2010).

We only included fixed effects other than the trait mean (μ) when they had previously been shown to have a predictable effect on a trait. This was done because the inclusion of fixed effects in an animal model can inflate the estimate of R and h^2 by reducing V_R (Wilson, 2008). Specifically, we included SVL as a fixed effect for trappability models, in that it has a positive effect [e.g., Rodda et al., 2007; Boyarski, Savidge, & Rodda, 2008; Tyrrell et al., 2009; but see also Engeman & Vice (2001) for no effect of SVL on trappability]. Therefore, estimates of h^2 for trappability represent the proportion of V_P that is due to V_A, after accounting for the effect of SVL on V_R. We included body condition, age, and trappability as fixed effects in models of annual mating success because they demonstrated significant partial effects in both sexes (**CHAPTER 1**). Similar to trappability, estimates of h^2 for mating success therefore represent the proportion of V_P due to V_A after conditioning on the effects of body condition, age, and trappability on V_R. We did not include additional fixed effects for models of SVL or body condition.

MCMCglmm requires that priors for variance components be specified. While these are but weakly informative, the choice of prior is not trivial and can have implications for the unbiased estimation of variance components. Therefore, we ran *MCMCglmm* with two different priors for each trait, so as to test the sensitivity of our variance component estimates with regard to prior specifications (see APPENDIX). With the first prior, we assumed the observed phenotypic variance of a trait was due in equal parts to additive (~33.3%), permanent environment (~33.3%), and residual effects (~33.3%). A low degree of belief was applied to these assumptions (n=0.2; Taylor et al., 2012). With the second prior, we assumed that observed phenotypic variance was primarily due to an additive genetic effect (95%), and less to permanent environment (2.5%) and residual effects (2.5%), with a corresponding low degree of belief (n=0.2).

We also tested the sensitivity of estimates with regard to the "connectedness" of the pedigree. Estimates of additive genetic variance should be more precise if additional related individuals are included in a pedigree (Wilson et al., 2010). Therefore, we tested both prior settings against two versions of our pedigree: (1) One with known individuals only [N=426; APPENDIX FIGURE S1(A)], and (2) one with known individuals plus 73 dummy individuals assigned by *Sequoia* [N=499; APPENDIX FIGURE S1(B)]. Inclusion of dummy parents decreases the number of individuals assumed to be unrelated, thereby allowing half-siblings without sampled parents as components of the additive genetic relationship matrix (i.e., the A matrix; Kruuk, 2004). Yet, because dummy individuals represent only hypothesized pedigree links, it was prudent to ascertain whether their inclusion impacted variance component estimates.

To produce adequate effect sizes, MCMC chains were run for 5,000,000 to 6,000,000 iterations with a thinning interval of 1,500 to 2,500 to minimize autocorrelation, and a burn-in of 50,000 iterations to ensure convergence (see APPENDIX TABLE S1 for specifics for each trait model). We applied the *autocorr.diag* function of the *R* package *coda* (Plummer, Best, Cowles, & Vines, 2006) to confirm that autocorrelation values at first thinning were less than 0.1 (APPENDIX TABLE S2; de Villemereuil, 2012). We visually inspected trace plots for chain convergence and also empirically tested for convergence using Heidelberger and Welch's convergence diagnostic, with all models compliant (*P*>0.05). Finally, we visually inspected density plots of the posterior distributions for multiple peaks and checked that the sizes for all random effects exceeded 1000 (APPENDIX TABLE S2; de Villemereuil, 2012).

Variance component point estimates were taken as the mode of the posterior distribution (Wilson et al., 2010), with 95% confidence intervals (CIs) calculated as the 95% highest posterior density interval (HPD), using the *HPDinterval* function of the *R* package *coda*

(Plummer et al., 2006). We derived R for each trait by dividing the sum of V_A and V_I by V_P, while h^2 for each trait was calculated by dividing V_A by V_P. We also calculated 95% CIs for our estimates of *R and* h^2.

Given appropriate priors, variance components estimated with *MCMCglmm* are constrained to be positive (Wilson et al., 2010). Therefore, the significance of parameter estimates could not be estimated by gauging the overlap of their 95% CIs with zero. Instead, we fitted models without the random effect(s) of interest, but with the other random effects retained, such that the deviance information criteria of the reduced model (DIC; Spiegelhalter, Best, Carlin, & Van Der Linde, 2002) could be compared with the global model containing the random effect(s) of interest (Ariyomo, Carter, & Watt, 2013; Wilson et al., 2010). DIC is a Bayesian alternative to Akaike Information Criteria (AIC), and a smaller DIC value indicates a preferred model (per AIC; Ellison, 2004). For each trait, the significance of R was determined by fitting models without the “individual” and “animal” terms, but with the “residual” term retained, as R is equal to the sum of V_I and V_A divided by V_P. To test the significance of h^2, we fit models without an “animal” term while retaining “individual” and “residual” terms. All analyses were conducted in either *RStudio* (*R v. 3.5.0*; RStudio Team, 2015) or *R* (*R v. 3.4.3*; R Core Team, 2013).

RESULTS

Sensitivity Analyses for the Animal Model—

The choice of priors for *MCMCglmm* had a negligible impact on variance estimation (APPENDIX TABLE S3). Parameter estimates were similar regardless of the prior setting, and all differences among estimates derived from the two priors were within the range of sensitivity analyses reported in other heritability studies (e.g., Patrick, Charmantier, & Weimerskirch 2013; Jenkins, Vitousek, Hubbard, & Safran 2014; Carrete et al., 2016). Parameter estimates were also robust to pedigree connectedness, with similar estimates derived from only known individuals versus the pedigree including 73 dummy individuals (APPENDIX TABLE S3). Further, parameter estimates as derived from the two pedigrees experienced similar levels of sensitivity with regard to the two priors. In contrast to other parameter estimates, the h^2 of mating success was more sensitive to the choice of prior when the less connected pedigree (i.e., without dummy individuals) was used to construct the A matrix. However, the difference was modest and fell within the range of values recorded in other studies (e.g., Patrick, Charmantier, & Weimerskirch 2013; Jenkins, Vitousek, Hubbard, & Safran 2014; Carrete et al., 2016). All parameter estimates reported and discussed below were therefore derived from the pedigree containing 73 dummy individuals [Appendix Figure S1(B)], and by using the weak prior that assumed equal contributions of V_A, V_I, and V_R to V_P, with a low degree of belief (APPENDIX).

Animal Model Parameter Estimates—

Estimates of R were variable, with some traits exhibiting high repeatability across years (TABLE 1). Mating success had especially high repeatability (~58.9%), particularly when juxtaposed with the next most repeatable trait (SVL~20.8%). However, all traits with the exception of trappability were significantly repeatable (TABLE 2).

Yet, estimates of h^2 were low for each trait (TABLE 1). Annual trappability had the highest heritability (~5.0%), while annual mating success had the lowest (~1.6%). Importantly, only body condition and trappability had significant V_A, and by consequence, significant h^2 (TABLE 2).

DISCUSSION

Effective management of invasive species requires an understanding of the short- and long-term consequences of control. In this sense, evaluating the potential for adaptive evolution as a response to control can help gauge whether efficacy is maintained over time (Závorka et al., 2018). Furthermore, if traits influenced by control are considered with respect to reproductive fitness, then the impact of control on population vital rates (e.g., birth rate) allows for a more nuanced perspective on the long-term ramifications of management.

In this study, we found two traits with low but statistically significant heritabilities [i.e., annual trappability (h^2=0.050), and annual body condition (h^2=0.035; TABLE 1)]. Both have a positive effect on male and female annual mating success, and thus, annual reproductive success (**CHAPTER 1**). Trapping is a primary aspect of BTS management on Guam (Rodda et al., 2007), and variability in trap-response among individuals, as well as the consistent selective pressure exerted by traps, have prompted questions relating to the heritability of trappability (Tyrrell et al., 2009). We found low but statistically significant V_A for trappability after adjusting for the known effects of SVL on V_R [TABLES 1 and 2(B)]. Although direct studies of the heritability of trappability are few (e.g., Cooke et al., 2007; Waples & Naish, 2009), those focusing on boldness have been more prominent [i.e., sustainable harvest (Alós, Palmer, Trías, Díaz-Gil, & Arlinghaus, 2015) and invasive species research (Bravener & McLaughlin, 2013; Evangelista, Britton, & Cucherousset, 2015)]. Boldness is positively correlated with trappability across taxa (Biro & Dingemanse, 2009), and also reflects significant heritability in a variety of systems [e.g., Bridge Spider (Kralj-Fišer & Schneider, 2012); Zebra Fish (Ariyomo et al., 2013), Wandering Albatross (Patrick et al., 2013); Bighorn Sheep (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009)]. In fact, trappability has often been used as a surrogate for boldness (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; Wilson, Coleman, Clark, & Biederman, 1993). Given behavioral differences noted in BTS with regard to trappability (Tyrrell et al., 2009), it is not surprising that this trait also displays significant heritability as well.

Although heritability was low, it is nonetheless disconcerting for BTS management in that the consistent selective pressure from trapping can promote adaptive evolution such that individuals become less trappable over time. A similar result has been documented in fishes (Cooke et al., 2007). Yet, we previously found that trappability has a positive effect on annual mating success in BTS, and by consequence, annual reproductive success (**CHAPTER 1**). Therefore, if less trappable BTS are positively selected for, then the population birth rate may be suppressed (given its effects on annual mating success), representing a potential silver lining to the heritability of trappability.

We also found body condition, or more technically, unmeasured traits that affect body condition, to have low but statistically significant heritability [TABLE 2(B)]. Again, this is somewhat concerning in that we previously found directional selection on body condition to be significantly positive during years of (or subsequent to) high prey availability, a situation that can arise in response to management actions (**CHAPTER 2**). For example, intense trapping can depress population size in BTS, allowing prey to subsequently increase in numbers (Yackel Adams et al., unpublished data). Positive selection during times of high prey availability may promote traits values that contribute to good body condition, possibly bolstering the population against negative effects of future prey declines. Furthermore, we previously found that body condition had a significant positive effect on annual mating success in both sexes, thus impacting annual reproductive success (**CHAPTER 1**). In this sense, evolution of traits that improve body condition in response to post-trapping prey densities would promote elevated average reproductive success.

We did not identify significant heritabilities for SVL or mating success, although both were significantly repeatable from year to year [TABLES 1 and 2(A)]. We were particularly intrigued that annual mating success had the highest repeatability of all traits examined (R=0.589), meaning that individuals are iterative from year to year in the number of mating partners from which offspring are produced. Yet, heritability of mating success was not statistically significant (h^2 after conditioning on fixed effects=0.016) [TABLE 2(B)]. Consistent individual differences in mating success from year to year were instead due to individual permanent effects [V_I (e.g., maternal or birth year effects (Wilson et al., 2010)], as well as age, body condition, and trappability effects (**CHAPTER 1**).

Regardless, the repeatability of mating success may have substantial implications for evolution of BTS as it pertains to control. Annual mating success is a significant determinant of annual reproductive success for both sexes (**Chapter 1**), such that individuals with more mates in a given year produce more offspring. Selection on mating success is strongest during years of low prey availability (e.g., due to prey suppression; Christy et al., 2017), favoring individuals with higher mating success (**Chapter 2**). Because individuals have similar annual mating success each year (i.e., with high repeatability), a similar set of individuals with elevated mating success will produce the most offspring during years of strong selection and contribute the most alleles to the following generation, resulting in micro-evolutionary change over time (Gompert et al., 2014). In support of this notion, we previously found that genetic diversity of offspring in the study population was highest during years of stronger selection on annual mating success (**Chapter 2**).

We offer three possible (and not exclusive) scenarios regarding the low estimates of heritability for each trait evaluated. First, the estimated heritability of a trait is affected to some degree by the fixed effects included in the animal model. This is because fixed effects reduce V_R and therefore increases the proportion of V_P due to V_A (Wilson, 2008). In this study, we only included fixed effects when they were known to have a predictable effect on the traits of interest. This was done so as to avoid an overestimation of narrow-sense heritabilities. Therefore, it is possible that our estimates of heritability are overly conservative.

Second, heritabilities are not constant (Visscher, Hill, & Wray, 2008), but are instead specific to the individuals involved in their derivation. To maximize statistical power, we included all repeated measures of individuals. In some cases, sampling episodes encompassed the entire lifespan of an individual (i.e., first sampled during juvenile years then repeatedly sampled during sub-adult and adult years). Had we partitioned our data by age class, we may have discerned different heritabilities for those same traits when individuals were juveniles versus adults, in that fewer individuals survive to adulthood than are born (e.g., Réale et al., 1999). However, additional sampling would be required to attain a sample size necessary to estimate heritabilities by age class. Third, it is also possible that low V_A is simply due to BTS being founded via a single, small invasion event on Guam (i.e., genetic bottleneck; Richmond et al., 2014). In this sense, future work can test hypotheses regarding the origin of low V_A estimates in the study population.

In conclusion, we identified two traits important for reproduction in BTS that are significantly governed, at least in part, by additive genetic variation. This, in turn, highlights the potential response of these traits to strong selective pressures, as imposed by control methods. Furthermore, these traits have significant effects on annual mating success, and by consequence, annual reproductive success. Our study therefore demonstrates the potential for adaptive evolution of BTS traits, as promoted by current control measures, that could shift the average annual reproductive success of the study population.

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APPENDIX

Tables—

TABLE 1. Additive genetic variance (V_A), individual variance due to permanent environment effects (V_I), residual variance (V_R), total phenotypic variance (V_P), repeatability (R), and narrow-sense heritability (h^2) are summarized for four traits [i.e., body condition, trappability (i.e., propensity to enter baited traps), snout-vent length, and mating success (i.e., number of mates with which an individual produces offspring)] important to reproductive success and affected by the control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. Weakly informative priors assumed that V_A, V_I, and V_R equally comprised V_P, with a low degree of belief (nu=0.2). The pedigree (N=499) included 73 dummy parents that served to link generations when groups of half-siblings did not display a sampled parent. Parameter estimates reflect 95% highest posterior density (HPD) intervals.

Parameter	Body Condition	Trappability	Snout-Vent Length	Mating Success
V_A	0.001 (0.000 - 0.003)	0.169 (0.070 - 0.339)	1014.058 (347.466 - 3154.953)	0.021 (0.004 - 0.553)
V_I	0.002 (0.000 - 0.004)	0.108 (0.048 - 0.222)	6,905.207 (4,318.856 - 11,423.730)	0.833 (0.018 - 1.356)
V_R	0.032 (0.029 - 0.035)	2.496 (1.986 - 2.920)	37,049.047 (33,800.500 - 41,249.020)	0.638 (0.093 - 1.236)
V_P	0.035 (0.033 - 0.039)	2.645 (2.275 - 3.263)	47,493.660 (42,846.860 - 51,079.130)	1.630 (1.088 - 2.276)
R	0.091 (0.051 - 0.157)	0.095 (0.052 - 0.149)	0.208 (0.128 - 0.266)	0.589 (0.271 - 0.882)
h^2	0.035 (0.012 - 0.098)	0.050 (0.026 - 0.119)	0.021 (0.006 - 0.065)	0.016 (0.002 - 0.339)

TABLE 2. Additive genetic variance (V_A), individual variance due to permanent environment effects (V_I), residual variance (V_R), total phenotypic variance (V_P), repeatability (R), and narrow-sense heritability (h^2) were derived for four traits [body condition, trappability (i.e., propensity to enter baited traps), snout-vent length, mating success (i.e., number of mates with which an individual produces offspring] important to reproductive success and affected by control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. Priors assumed V_A, V_I, and V_R equally comprised V_P, with a low degree of belief (nu=0.2). The pedigree (N=499) used in the animal model included 73 dummy parents that served to link generations when groups of half-siblings did not display a sampled parent. Statistical significance of (A) R and (B) h^2 were evaluated for each trait by comparing the deviance information criteria (DIC) of models with and without the random effect(s) of interest with other random effects retained. Lower DICs (in bold) indicate the preferred model.

(A)

	Deviance Information Criteria			
	Body Condition	Trappability	Snout-Vent Length	Mating Success
With V_A or V_I	**-595.243**	2565.160	**965.119**	**965.119**
Without V_A or V_I	-568.449	**2540.169**	15336.800	969.135

(B)

	Deviance Information Criteria			
	Body Condition	Trappability	Snout-Vent Length	Mating Success
With V_A	**-595.243**	**2565.160**	965.119	965.119
Without V_A	-588.632	2566.467	**963.855**	**963.855**

MCMCglmm Priors and R Code—

Explanation of *MCMCglmm* Priors:

Prior 1: Phenotypic variation split evenly between additive genetic, individual permanent environment, and residual variance components with a low degree of belief (n = 0.2).

Prior 2: 95% of phenotypic variance is due to the additive genetic effect, with the remaining 5% of phenotypic variance due evenly to individual permanent environment (2.5%) and residual (2.5%) effects, with a low degree of belief (n = 0.2).

R Code for *MCMCglmm* Priors:

Prior 1: `list(G = list(G1 = list(V = matrix(p.var/3), nu = 0.2), G2 = list(V = matrix(p.var/3), nu = 0.2)), R = list(V = matrix(p.var/3, nu = 0.2)`

Prior 2: `list(G = list(G1 = list(V = matrix(p.var * 0.95), nu = 0.2), G2 = list(V = matrix(p.var * 0.025), nu = 0.2), R = list(V = matrix(p.var * 0.025), nu = 0.2)`

*Note: p.var = phenotypic variance of the trait as estimated from the data

Supplemental Figures and Tables—

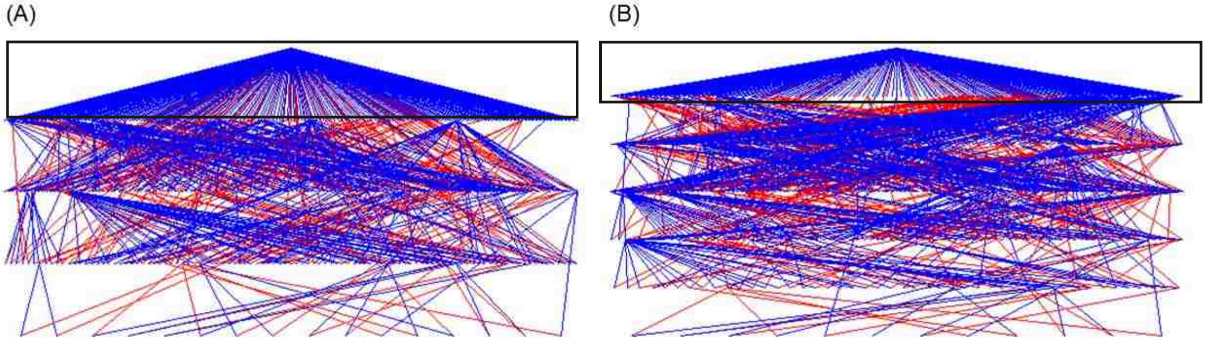

FIGURE S1. Two different but related pedigrees were used to reconstruct additive genetic relationship matrices (i.e., A matrices) for animal models of four traits [i.e., body condition, trappability (propensity to enter baited traps), snout-vent length, mating success (number of mates with which an individual produced offspring)] important to reproductive success and affected by control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. Pedigrees included either (A) only known individuals in the study population (N=426), or (B) known plus dummy individuals (N=73) that served to link generations when groups of half-siblings did not display a sampled parent. Each pedigree reflects depth (i.e., number of connected, consecutive generations) rather than cohorts, as cohorts of dummy individuals are unknown. Lines represent links between male (blue) or female (red) Brown Treesnakes and their offspring. Both pedigrees assume that the earliest links in consecutive generations are founders (denoted by black boxes), and individuals without known or dummy parents are unrelated to all others in the population. Note the greater depth of the pedigree in (B).

TABLE S1. Settings for *MCMCglmm* models of four traits [i.e., body condition, trappability (propensity to enter baited traps), snout-vent length, mating success (number of mates with which an individual produced offspring)] important to reproductive success and affected by the control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. Models were run (=Iterations) with Gaussian or Poisson error distributions (=Distribution) to produce adequate effect sizes, with thinning intervals (=Thinning) to minimize autocorrelation, and a burn-in (=Burn-In) to ensure chain convergence.

Trait	Distribution	Iterations	Thinning	Burn-In
Body Condition	Gaussian	5,000,000	1,500	50,000
Trappability	Poisson	5,000,000	1,500	50,000
Snout-Vent Length	Gaussian	5,000,000	1,500	50,000
Mating Success	Poisson	6,000,000	2,500	50,000

TABLE S2. The *R* package *MCMCglmm* was used to estimate additive genetic variance (V_A), individual permanent environment variance (V_I), residual variance (V_R), total phenotypic variance (V_P), repeatability (*R*), and narrow-sense heritability (h^2) of four annual traits [body condition, trappability (i.e., propensity to enter baited traps), snout-vent length, mating success (i.e., number of mates with which an individual produces offspring] important to reproductive success and affected by control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. Weakly-informative priors assumed that V_A, V_I, and V_R equally comprised V_P, with a low degree of belief (nu=0.2). The pedigree (N=499) was reconstructed with the *R* package *Sequoia* and included 73 dummy parents that served to link generations when groups of half-siblings did not display a sampled parent. For each parameter estimate of each model, autocorrelation was tested for via the *autocorr.diag* function of the *R* package *coda* to ensure that autocorrelation values (=AC) at the first thinning were <0.1. Effect sizes (=ES) were derived to ensure that values were $\geq$1000.

	V_A		V_I		V_R		V_P		*R*		h^2	
Trait	AC	ES	AC	ES	AC	ES	AC	ES	AC	ES	AC	ES
Body Condition	0.01	3300.00	0.03	3100.51	0.02	3300.00	-0.01	3300.00	0.07	2898.91	0.01	3300.00
Trappability	-0.01	3300.00	-0.01	3300.00	-0.02	3465.52	-0.03	3484.40	0.01	3300.00	-0.01	3300.00
Snout-Vent Length	-0.01	3300.00	0.00	3300.00	-0.02	3300.00	0.00	3300.00	-0.03	3483.68	0.00	3300.00
Mating Success	0.04	1698.62	0.02	2380.00	0.00	2380.00	0.00	2380.00	0.03	2241.70	0.03	1964.68

TABLE S3**.** The *R* package *MCMCglmm* was used to estimate additive genetic variance (V_A), individual variance due to permanent environment effects (V_I), residual variance (V_R), repeatability (R), and narrow-sense heritability (h^2) of four traits (panels A–D) important to reproductive success and affected by control of an experimentally-closed population of invasive Brown Treesnake (*Boiga irregularis*) in northern Guam. The sensitivity of parameter estimates to the connectedness of the pedigree was tested for by using either a pedigree containing only known individuals (=Ped 1; N=426), or known plus 73 dummy individuals (=Ped 2; N=499) used to construct the additive genetic relationship matrix (i.e., A Matrix). We also tested the sensitivity of parameter estimates to the *MCMCglmm* prior settings (Prior 1 = V_P due equally to additive genetic, individual permanent environment, and residual effects with low degree of belief (nu=0.2); Prior 2 = V_P due primarily to additive genetic effect (=95% V_P) and in small part to individual permanent environment (=0.025% V_P) and residual (=0.025% V_P) effects with low degree of belief (nu=0.2).

(A) Body Condition

	V_A		V_I		V_R		R		h^2	
	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2
Prior 1	0.001	0.001	0.002	0.001	0.032	0.032	0.090	0.091	0.022	0.035
Prior 2	0.001	0.002	0.000	0.000	0.033	0.033	0.074	0.080	0.044	0.066

(B) Trappability

	V_A		V_I		V_R		R		h^2	
	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2
Prior 1	0.159	0.169	0.109	0.108	2.429	2.496	0.092	0.095	0.053	0.050
Prior 2	0.198	0.231	0.024	0.022	2.489	2.637	0.097	0.101	0.087	0.080

(C) Snout-Vent Length

	V_A		V_I		V_R		R		h^2	
	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2
Prior 1	1033.093	1014.058	8040.333	6905.207	36928.468	37049.047	0.204	0.208	0.019	0.021
Prior 2	1679.474	1697.745	7875.839	7368.129	38526.398	37996.492	0.194	0.202	0.034	0.038

(D) Mating Success

	V_A		V_I		V_R		R		h^2	
	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2	Ped 1	Ped 2
Prior 1	0.027	0.021	0.498	0.041	0.543	0.638	0.686	0.589	0.020	0.016
Prior 2	0.164	0.127	0.008	0.001	0.652	0.639	0.601	0.547	0.141	0.046

Conclusion

Invasive species are a major threat not only to biodiversity (Simberloff, 2001), but also the global economy (Olson, 2006) and human health (Juliano & Lounibos, 2005). As a means to improve control, myriad studies have focused on invasive species biology in particular, and the dynamics of invasion in general (Andersen, Adams, Hope, & Powell, 2004; Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015; Kolar & Lodge, 2002). Yet, control measures can also be a source of considerable selective pressure on invasives (i.e., “anthropogenic selection;” Santamaría & Méndez, 2012), and this can drive vital rates, genetic variability, and evolutionary trajectories of those traits so selected, with subsequent outcomes difficult to predict over time. What is required in the context of invasive species control is the application of evolutionary concepts (in addition to those ecological), but unfortunately this approach is only beginning to develop (Cook & Sgrò, 2017).

In this context, I employed an evolutionary approach to the management of invasive Brown Treesnake by: (1) Characterizing fundamental aspects of its reproductive ecology, (2) measuring selection on traits identified as important for mating and reproduction, (3) assessing the role of selection in shaping population genetic variation, (4) gauging the potential for these traits to evolve in response to control, and (5) underscoring the effect of potential trait evolution on average annual reproductive success. Importantly, the temporal dynamics of BTS reproductive ecology were placed within the context of “evolutionary enlightened management” (Ashley et al., 2003), and as such, serve as a benchmark for control efforts.

In **CHAPTER 1**, I characterized the mating system of the Brown Treesnake on Guam and identified those traits that impact its annual mating and reproductive success. To do so, I constructed a 15-year pedigree for the study population using 654 highly informative single nucleotide polymorphisms (SNPs) derived from double digest restriction-site associated DNA (ddRAD) library preparation. The pedigree allowed for individual mating and reproductive success to be estimated annually, and revealed the genetic mating system of the study population to be promiscuous. Both sexes demonstrated significant positive effects with regard to the impacts of body condition, age, and trappability on annual mating success, yet, each differed somewhat in traits that affected annual reproductive success. Males were influenced by mating success, age, and body condition, whereas mating success and age, but not body condition, positively influenced females, and with degree of inbreeding as a negative impact.

In **CHAPTER 2**, I estimated the annual strength of selection on each trait identified as important for annual mating and reproductive success (per **CHAPTER 1**). I also evaluated the manner by which selection varied temporally on these traits, then tested for a relationship between strength of selection and the genetic variability of offspring produced during the year of selection. I then juxtaposed patterns of selection against control measures applied within the population that affected prey availability. There was significant temporal variation in the annual effect of age on mating success, as well as mating success on reproductive success. Annual selection gradients for mating success were significant in both sexes across each year of the study. There was also a positive relationship between the strength of selection on female mating success and the genetic variability of offspring born during the year of selection. Those years with (or subsequent to) low prey availability for adults elicited significantly greater selection on annual mating success. Thus, prey suppression may have manifold effects. It may diminish the potential for reproduction on one hand (Yackel Adams et al., unpublished data), yet on the other it can bolster the evolutionary potential of BTS.

In **CHAPTER 3**, I estimated the repeatability, additive genetic variance, and narrow-sense heritability of traits important for annual mating and reproductive success in both sexes. These were: Body condition, snout-vent length, trappability, and mating success. All traits varied in their repeatability, but with greatest values recorded for annual mating success. Only body condition and trappability had significant additive genetic variance, and by consequence, significant narrow-sense heritability. Considering the significant effect of body condition and trappability on annual mating success, and the relationship between these traits and control methods, body condition and trappability have the capacity to evolve in response to selection imposed by control. This response could clearly impact population birth rate.

The results of this study yielded unprecedented insight into the reproductive ecology of BTS, a previously opaque research agenda due in large part to the cryptic behavior of the species. Further, this study is the first to explicitly gauge the reproductive ecology of BTS with regards to population genetic variability, trait heritability, and selection imposed by control, and it did so in the context of ongoing management. The results of this study will promote "evolutionarily enlightened management" (Ashley et al., 2003) in a general context, and specifically with regards to the invasive Brown Treesnake on Guam.

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Appendix

IACUC Approval Letter

All samples were collected by the United States Geological Survey Brown Treesnake Project, but the following IACUC protocol allowed Brenna Levine to participate in sampling during the summer of 2016.

UNIVERSITY OF ARKANSAS

Office of Research Compliance

MEMORANDUM

TO: Marlis Douglas
FROM: Craig N. Coon, Chairman
DATE: May 6, 2016
SUBJECT: IACUC Approval
Expiration Date: May 5, 2017

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # 16063 "Kinship, Reproductive Output, and Genetic Components of Trappability in the Invasive Brown Treesnake (Colubridae: Boiga irregularis) on Guam, with Implications for Control and Management ".

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond May 5, 2017 you must submit a modification or new protocol prior to that date to avoid any interruptions. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

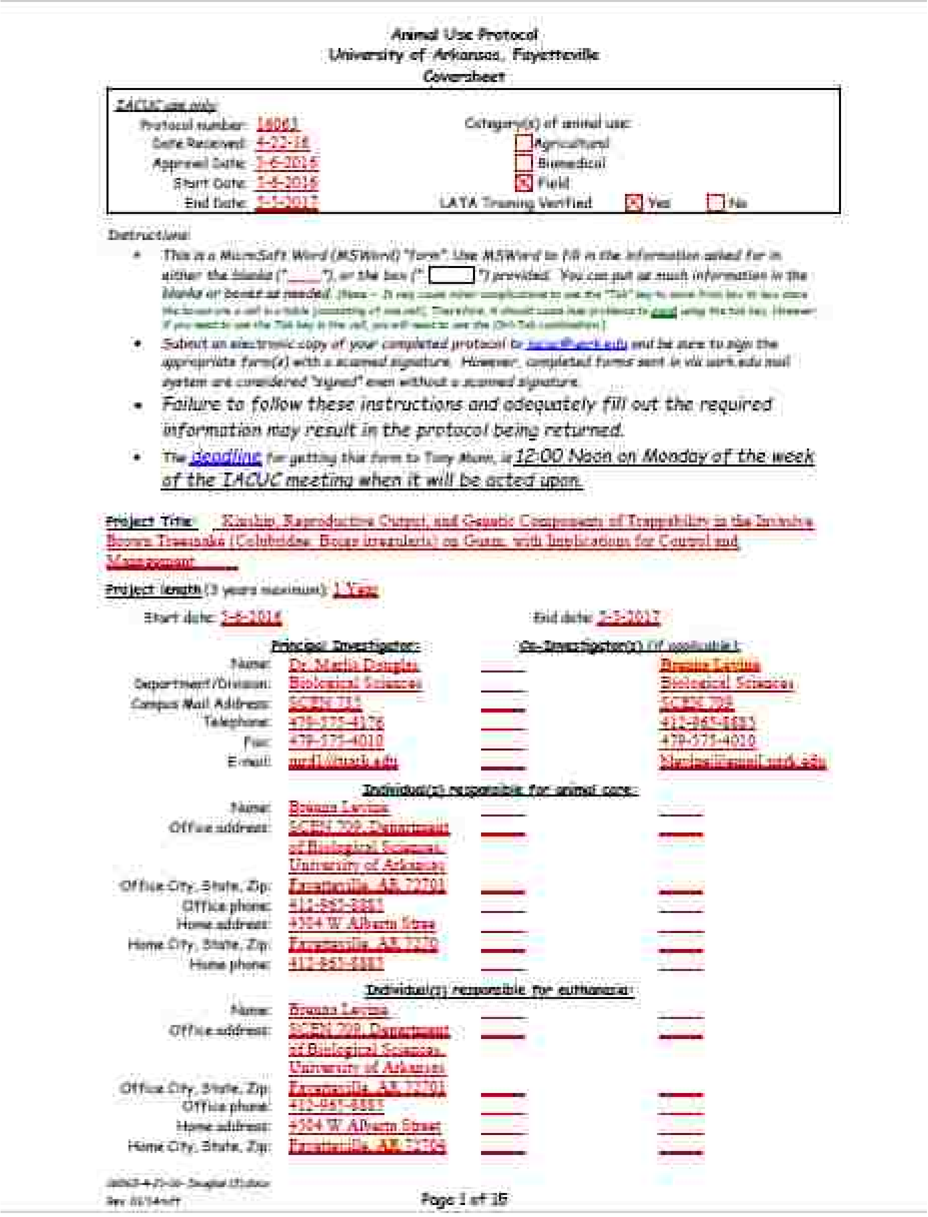
CNC/aem

cc: Animal Welfare Veterinarian

Administration Building 210 • 1 University of Arkansas • Fayetteville, AR 72701-1201 • 479-575-4572
Fax: 479-575-3846 • http://vpred.uark.edu/199

IACUC PROTOCOL COVERSHEET

The following coversheet is on file with IACUC, and shows that Brenna A. Levine is the co-investigator on the IACUC protocol.



Animal Use Protocol
University of Arkansas, Fayetteville
Coversheet

IACUC use only:
Protocol number: 16063
Date Received: 4-22-16
Approval Date: 5-6-2016
Start Date: 5-6-2016
End Date: 5-5-2017

Category(s) of animal use:
☐ Agricultural
☐ Biomedical
☒ Field

LATA Training Verified ☒ Yes ☐ No

Instructions:

- *This is a MicroSoft Word (MSWord) "form". Use MSWord to fill in the information asked for in either the blanks ("____"), or the box (" ☐ ") provided. You can put as much information in the blanks or boxes as needed.*
- *Submit an electronic copy of your completed protocol to iacuc@uark.edu and be sure to sign the appropriate form(s) with a scanned signature. However, completed forms sent in via uark.edu mail system are considered "signed" even without a scanned signature.*
- *Failure to follow these instructions and adequately fill out the required information may result in the protocol being returned.*
- *The deadline for getting this form to Tony Munn, is 12:00 Noon on Monday of the week of the IACUC meeting when it will be acted upon.*

Project Title: Kinship, Reproductive Output, and Genetic Components of Trappability in the Invasive Brown Treesnake (Colubridae: Boiga irregularis) on Guam, with Implications for Control and Management

Project length (3 years maximum): 1 Year

Start date: 5-6-2016
End date: 5-5-2017

	Principal Investigator:		Co-Investigator(s) (if applicable):
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Individual(s) responsible for animal care:

Name:	Brenna Levine		
Office address:	SCEN 709, Department of Biological Sciences, University of Arkansas		
Office City, State, Zip:	Fayetteville, AR 72701		
Office phone:	412-965-8883		
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Home City, State, Zip:	Fayetteville, AR 7270		
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Individual(s) responsible for euthanasia:

Name:	Brenna Levine		
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Rev. 01/14

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