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CHAPTER 9

Behavioral Ecology of Aggressive Behavior in Lizards

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CONTENTS

INTRODUCTION

Aggression in lizards has been a central focus of a wide range of studies because so many species experience intense sexual selection and/or competition over limited resources. Furthermore, many lizards are brightly colored, defend territories in open spaces where they are easy to observe, and allow close approach, making them particularly amenable to study (Fox et al. 2003). Aggressive behavior has been studied in the context of endocrine and physiological control (Chapter 6), signaling (Chapters 3 and 7), rival recognition, access to resources and mates by both sexes, and with respect to social systems (Chapter 10). This chapter reviews the behavioral ecology of aggression at the individual, population, and species levels, and identifies areas where lizards could be a suitable model system for addressing the influence of aggression on fitness more broadly. Our chapter has four key goals. First, we describe aggression, patterns of aggressive behavior in lizards, and how studies of lizards have contributed to animal behavior theory more broadly. Second, we briefly explain the mechanisms that underlie aggression and the emergence of aggression during development. Third, we review the evolutionary function of aggression in different contexts, including natural selection (e.g., survival, acquisition of resources), sexual selection (e.g., competition for mates) and social selection (e.g., kin effects). Finally, we discuss the potential implications of aggression for the ecological and evolutionary trajectory of populations.

PART I: AGGRESSION AND BEHAVIOR

Aggression hardly needs a definition because it is so ubiquitous and pervades so much of animal and human social behavior. For the purposes of this chapter, aggression is any negative behavior that is directed at one or more individuals that imposes a cost to that individual, either in the short-term (e.g., increased stress) or the long-term (e.g., reduced fitness). Aggressive behavior is a double-edged sword, because while the outcome may be favorable if it results in an animal securing a territory, or keeping a rival from a mate (mate guarding) or a resource, there is a physiological cost to being aggressive (Chapter 10). From a behavioral standpoint, aggression is particularly interesting because it may be exaggerated to bluff a rival or deter a predator and may not be an honest signal (Chapters 3 and 7). In the case of aggressive behavior directed at a predator, species with deimatic displays may use aggression to amplify the effect of a startle display (Umbers et al. 2017). For example, Bluetongue lizards (*Tiliqua* spp.) use aggressive defensive behavior when they expose their UV-blue tongues at predators (Badiane et al. 2018). The interaction of a startle display and aggression, whereby the display is amplified by an aggressive behavioral response, is particularly

important in these species. Empirical evidence for deimatic displays is starting to accumulate in light of recent theoretical developments (Umbers et al. 2017) and lizards show great promise as a model system.

DESCRIPTIONS OF AGGRESSIVE BEHAVIOR AND SIGNALING

In lizards, aggression is indicated either directly using static and/or dynamic visual signals (Whiting et al. 2003) or indirectly through chemical signals (López and Martín 2002; Carazo et al. 2007, 2008) (Chapter 7). In many species, both visual and chemical signals are used together (Lopez et al. 2003; Whiting et al. 2009) and in the context of aggression, it is likely that visual and chemical signals reinforce the same message (Martin and Lopez 2010; Whiting et al. 2009). For example, chemical scent may be deposited on a substrate and signal territory ownership (Carazo et al. 2007, 2008), or it may be used in close encounters with rivals (Whiting et al. 2009). Conversely, whereas visual signals are also used in close encounters, they are typically effective at a greater distance than chemical scents (Whiting et al. 2009). Many species that experience strong sexual selection signal aggression through colorful displays while also conveying information about fighting ability through femoral gland secretions. Consequently, lizards are a particularly useful model system for studying multimodal signaling.

Aggressive displays have been described for a wide range of species, beginning with Charles Carpenter's seminal work on North American lizards (Carpenter 1977). Many species typically use a graded aggressive response when confronted by a conspecific rival. In this scenario, the level of aggressive response increases in direct proportion to the level of threat, assuming that both rivals are signaling honestly to one another (Whiting et al. 2003). Under particular circumstances, lizards will respond with an aggressive chase without any signal. This is the case in the Augrabies Flat Lizard (*Platysaurus broadleyi*) when males see rivals at the last moment, when they are at relatively short distances from one another and/or on or close to a resident's territory. In these scenarios, a threat is immediately of high intensity. However, if they make visual contact at a distance and a rival is away from the boundary of its territory, they will first signal to a rival. Because aggression is costly in terms of energy expended and potential for injury, males typically signal their status to avoid fights with a predictable outcome, such as when two males have a pronounced asymmetry in status. When males are closer in size or dominance, or if they are contesting a high value resource, they are more likely to respond aggressively and fight. For most lizards, visual displays are followed by physical chases and biting if rival males fail to cede to their opponents in a contest. Lizards may have multiple armaments, such as throat color and belly patches, and these may convey different information (e.g., fighting ability and male quality)(Møller and Pomiankowski 1993) or they may serve to reinforce the same message (i.e., redundancy) (Rand and Williams 1970). The type of display used by males also may vary according to social context (Whiting et al. 2003).

Classic signals of aggressive behavior include inflating the body; exposing color patches (e.g. on ventrum); inflation of the throat; tail-flicking, waving, or curling; hand-waving; head-bobbing; standing upright and presenting the body laterally/back arching; gaping; and changing color (illustrated by Carpenter (1977). The Marine Iguana (*Amblyrhynchus cristatus*) engages in an unusual contest behavior involving male head-butting or shoving (Carpenter 1966a) reminiscent of ungulate contests. Males may also convey information on dominance or fighting ability using static traits such as body size (Tokarz 1985; Rodda 1992; Alberts et al. 2002), tail length (Carpenter 1967; Cooper 2001), elongated dorsal spines (Baird et al. 2012), frills (Shine 1990), extensible dewlaps (Nicholson et al. 2007), variation in head shape (Lappin et al. 2006), and color of dewlaps, throat fans, and frills. For many species, variation in color among males in a population indicates fighting ability or aggressive behavior (Molnár et al. 2016). Agonistic displays may also involve a simple

display such as a male taking a conspicuous position on an exposed or elevated perch (such as in the South Indian Rock Agama [*Psammophilus dorsalis*]) (Radder et al. 2006a, b).

PATTERNS OF AGGRESSIVE BEHAVIOR

Consistent Individual Variation in Aggression

A key question in behavioral ecology is how stable aggressive behavior is, and whether it represents a personality trait or if it is plastic or condition dependent. Studies of consistent individual variation in animals address whether a trait is consistent within individuals and across contexts while being variable among individuals (i.e., personality or behavioral type) (Bergmüller 2010). Of additional interest is whether the rank order of among-individual variation is consistent across contexts and when the environment changes. While there is great interest in, and evidence for, consistent individual varation in behavioral traits (Sih et al. 2004), behavior is also influenced by state, sex, and life history stage. In the case of aggression, reproductive state clearly influences aggression in both males and females. Nevertheless, some individuals are consistently more aggressive than others, even if there is temporal variation in their level of aggressiveness. Therefore, plasticity in behavior may in fact be constrained (Bergmüller 2010; Dingemanse et al. 2010). In the case of lizards, it is useful to ask whether aggression is a personality trait and if there are ramifications for any associated constraints.

Aggression is rarely measured as a personality trait in lizards—it is more common to measure boldness. Indeed, aggression and boldness are often correlated. Nevertheless, aggression has been assayed as a measure of consistent individual variation in a handful of lizard species. In the case of the family-living White's Rock Skink (*Liopholis whitii*), aggression was the most repeatable of five behavioral traits (aggression, boldness, exploration, sociability, activity) across two assays, and for both males and females (McEvoy et al. 2015). Aggression was measured by touching the lizard's snout up to ten times with a plasticine lizard model attached to a stick. Lizards responded with a range of behaviors from taking refuge to back arching, open-mouthed displays, and biting the model. While aggression was repeatable across the two assays, it did not correlate with any of the other behavioral traits measured (either within or between individual covariance) (McEvoy et al. 2015). Interestingly, in a related study in the same species, the authors assayed aggression in the field and during staged contests in the laboratory. Aggression was once again repeatable in the field study, but in the laboratory study, only winners showed consistency in aggressive behavior, whereas losers did not (McEvoy et al. 2012). Aggression was also assayed in another family-living lizard, the Tree-crevice Skink (*Egernia striolata*). Captive-born offspring were raised either alone or in a pair, and their behavior was assayed four times over a year. Within pairs, a dominant–subordinate relationship formed and subordinates became more aggressive over time, whereas dominant and solitary individuals were consistent in their aggressive responses (Riley et al. 2017).

In the monogamous Sleepy Lizard (*Tiliqua rugosa*), more aggressive males spent less time with their female partners, whereas less aggressive males were more strongly connected to their female partners in a social network, and more often in contact with them. This consistency in behavioral traits across contexts has been suggested to represent a behavioral syndrome in which "lovers" have stronger bonds with female partners than "fighters," which are more aggressive and have weaker bonds with their female partners (Godfrey et al. 2012).

Lizards are an excellent system for answering questions about consistent individual variation because they are easily assayed for aggressive responses either in the field or in the laboratory. Preliminary results, such as those described above, suggest that individuals may have only

limited flexibility in their levels of aggression. Data on more species will help establish whether this is a general finding. Finally, lizard species that show marked variation in personality offer an opportunity for studying the long-term effects of aggression and how it influences survival and reproductive success.

Lateralization and Aggression

Lateralization of the brain is well known in vertebrates and may be adaptive if it allows complementary behavior simultaneously, such as foraging while remaining vigilant for predators (Rogers 2000). The posterolateral placement of a lizard's eyes means that if a stimulus is presented directly anteriorly, they respond by turning the head to one side. This allows for field testing of lateralization in different contexts, such as aggression (Hews et al. 2004). Animals can also be tested for lateralization by covering individual eyes and testing responses in a similar way (Deckel 1995). Aggression has been demonstrated to have a left-eye bias in a wide array of vertebrates, including fishes, frogs, lizards, and mammals (Bisazza et al. 1998; Vallortigara 2000). In such cases, conspecific aggression elicits a stronger response when viewed from the left-visual field. Based on a study of seven individuals of the Green Anole (*Anolis carolinensis*) and three of the Brown Anole (*Anolis sagrei*) left eye preference was demonstrated for aggressive interactions in eight males and two females (Deckel 1995). In a follow-up study, 10 male *A. carolinensis* had either their left or right eyes covered, while 15 males did not. Both groups were involved in staged encounters and aggressive responses were more intense for the left side, although left eye aggression steadily increased with time in the case of the unmanipulated (15) lizards. Furthermore, assertion behavior was more heavily influenced by the left eye/right hemisphere (Deckel and Jevitts 1997). The Tree Lizard (*Urosaurus ornatus*) also uses a range of agonistic displays and has lateralized aggression, favoring the left visual field/right hemisphere (Hews and Worthington 2001). Not only males exhibit a left-eye bias during aggressive encounters: females of the Striped Plateau Lizard (*Sceloporus virgatus*) favor their left visual field when aggressively rejecting courting males once no longer receptive (Hews et al. 2004). The influence of lateralization on aggression in lizards is, however, greatly understudied, and has the potential to contribute to our general understanding of lateralization more broadly.

Aggression and Social Learning

Animals use social information to solve problems more quickly or to acquire key information about mates or resources in their environment, such as the location of a food source or suitable habitat patch (Cote et al. 2008; Cote and Clobert 2007; Clobert et al. 2009). Three species of lizard have thus far been tested for their social learning ability in an association task. The family-living Tree-crevice Skink (*Egernia striolata*) uses social information to short-cut individual learning (Whiting et al. 2018), whereas adults of the Eastern Bearded Dragon (*Pogona barbata*) use imitation of conspecifics (Kis et al. 2014). In the Eastern Water Skink (*Eulamprus quoyii*), young, but not old, males use social information to solve tasks (Noble et al. 2014). Given that adult male *E. quoyii* did not use social information, this raised the possibility that lizards may differentially use social information according to the relative dominance status of any two individuals. To test this hypothesis, contests were first staged between males in order to establish dominant–subordinate relationships between known individuals. Then, social learning tests were conducted in which one male in a pair was a demonstrator and either dominant or subordinate to the naïve learner. Surprisingly, control lizards learnt to solve the task as quickly as social learners, indicating that relative dominance had no influence on learning ability (Kar et al. 2017). The potential role of aggression and relative dominance in lizards is still an open question and deserving of attention.

PART II: DEVELOPMENT AND MECHANISMS UNDERLYING AGGRESSIVE BEHAVIOR

Age-Specific Aggression and the Development of Aggression through Life

It is well known that aggression is risky because it also serves to promote confrontation in which a "superior" rival will make the signaler pay the price if their fighting ability is lower than that of the receiver (Johnstone 1997). In birds, for example, there is social enforcement of dominance whereby aggressive behavior is constantly challenged and honest signaling is behaviorally enforced (Rohwer 1982). We are not aware of any example of social control of status signaling in lizards (reviewed by Whiting et al. 2003), but it is certainly plausible. If aggressive behavior is risky in part because it may attract attention from rivals, then the development or ontogeny of aggression, and the timing of its expression, is crucial. To this end, juveniles of many species begin to express some aggressive behavior toward other juveniles at an early age, although, with some exceptions, this dimension of behavioral development is particularly unstudied (Ruby and Baird 1993; Ballen et al. 2014; Stamps 1977b, Stamps 1978, Stamps and Krishnan 1994a, b, 1995, 1998; Fox et al. 1981). Much of what we know about juvenile lizard behavior and aggression is derived from a single study system, *Anolis aeneus* (the Bronze Anole). Judy Stamps conducted field studies and a series of important experiments (along with V.V. Krishnan) on this species to establish the ontogeny of territorial and aggressive behavior and the factors that determine social dominance during early life experiences. Because anoles use head-bobs to display, it is a straightforward task to measure display rates as an indicator of aggression, and it is also abundantly clear which individual in a dyad initiated an aggressive interaction. In an early study of ontogeny, Stamps (1978) found surprisingly high levels of aggression among juvenile *A. aeneus*, the intensity of which was dependent upon the size ratio between the juvenile resident and a tethered intruder. For *A. aeneus*, there is a clear ontogeny of display behavior and aggression. Juveniles, adult females, and adult males all have a similar repertoire of displays but use specific display types at different frequencies. What is perhaps most interesting about the results of Stamps' (1978) continuous study of juvenile behavior (i.e., ontogeny) in the field, is that juveniles begin with a large repertoire of displays and use particular displays less frequently as they develop. This is in contrast to the hypothesis that juvenile animals begin with limited display and social behavior repertoires, with these becoming more complex during the course of development. (This is more likely to be the case in animals that exhibit parental care.) In other words, adults of *A. aeneus* can be viewed as animals that have lost several of the displays they employed as juveniles. Stamps (1978) reported that "juvenile social systems are at least as complex and variable as are those of adults." In terms of ontogeny, juvenile males use fewer "fearful" displays as they mature, and females use fewer aggressive displays. The displays that juveniles use remain stereotyped in adults, with some exceptions—signature bobs are slightly shorter in juveniles. Also, some displays are more variable among juveniles, and the displays of juveniles morph into two forms: a courtship bob and a multibob. Importantly, aggression appears to be as critical for juveniles as it is for adults. Ontogeny of aggressive display has also been reported for *A. carolinensis* (Lovern and Jenssen 2001), in which juveniles give aggressive displays only during social interactions (i.e., they do not use broadcast signals). Juvenile males and females exhibit similar displays until they become "large," at which point males display at a higher rate, although these displays remain qualitatively most similar to those of adult females (Lovern and Jenssen 2001).

Anolis aeneus is notable for the importance of aggression during the juvenile stage and the stereotypy of many of its displays, and this may be so for other lizard species. In the Algerian Sand Lizard (*Psammodromus algirus*), more aggressive juvenile males secure larger home ranges, with more vegetative cover, and have higher short-term survival than do less aggressive ones (Civantos 2000). Early experience is potentially important for later social development, and aggression is a key component that drives social interactions (Ballen et al. 2014). For example, juveniles of the

Veiled Chameleon (*Chamaeleo calyptratus*) raised in isolation as opposed to being part of a group exhibited more subordinate behaviors than those raised in a group, although their overall levels of aggression were similar (Ballen et al. 2014). It is thought that defense of food is not, in fact, the primary reason for juvenile aggression (Stamps 1978). A more likely explanation is that aggressive interactions are important for future success and the acquisition of territories once juveniles reach adulthood. This could be the case if juveniles repeatedly challenge and dominate subordinates, making it less likely that the latter will attempt to secure space or resources in a particular area in the future (Stamps 1978).

Physiological Costs of Aggression: The Role of Testosterone

Lizards constitute a model system for understanding the influence of testosterone on aggression and social behavior and many studies have experimentally manipulated testosterone in free-living and captive lizards (Hews et al. 1994; Moore 1988b; Moore and Thompson 1990; Thompson et al. 1993; Weiss et al. 2002; Woodley and Moore 1999b; Stamps 1994; Sinervo et al. 2000; Fox 1983b). With higher levels of testosterone, males become more aggressive (Marler and Moore 1989; Fox 1983a; Moore 1988a; Moore 1986) and, in many species, more conspicuous (Marler and Moore 1988). They may also benefit from enhanced physiological performance (Sinervo et al. 2000) and acquire larger and/or superior home ranges (Fox 1983b; Sinervo et al. 2000). If aggression is accompanied by increased levels of testosterone, however, this may elevate metabolic rate and even compromise the immune system (Folstad and Karter 1992), although this is not always clear-cut (Roberts et al. 2004). Other costs associated with increased levels of testosterone and greater levels of aggression include reduced survival (Marler and Moore 1988), injury and a loss of social status in species for which tails signal status (Fox and Rostker 1982). Testosterone impacts a suite of traits that are all thought to bear on survival and fitness (Cox et al. 2009). Aggression can therefore be thought of as representing a physiological trade-off that may impact on life history and ultimately, fitness attributes (Sinervo and Svensson 1998).

PART III: THE EVOLUTIONARY FUNCTION OF AGGRESSION

Natural Selection

Female Aggression in Association with Access to Food and Resources

Compared to males, females of many lizard species frequently have similar, albeit reduced, traits, such as color patches. The function of such traits includes sex recognition, the stimulation of male courtship, the deterring of courting males when females are no longer receptive, and impacting intra-sexual competition for resources or mates (Baird 2004). Female aggression and territoriality, although typically less pronounced than in males, is still relatively common (Stamps 1977b). Aggression may manifest itself in territory defense or as a component of the structuring of a social hierarchy. To this end, female aggression has most commonly been documented in iguanids, but is encountered in many lizard families (Stamps 1977b). Whereas coloration or some phenotypic trait may be the attribute that signals female aggression or dominance, aggressive display behavior can serve the same function. Females of the Collared Lizard (*Crotaphytus collaris*) may be more aggressive and more likely to defend a territory in habitats that have fewer vantage points that are important for foraging (Baird and Sloan 2003). Competition for food also drives aggressive defense of territories by females of *Anolis aeneus*, which defend territories throughout the year (Stamps 1977a, 1978). Access to limited portions of habitat and, potentially, limited numbers of nesting sites, is likely to result in higher levels of female aggression. For example, females of the Common Green

Iguana (*Iguana iguana*) and the Marine Iguana (*Amblyrhynchus cristatus*) will aggressively compete for limited burrows and nest sites (reviewed by Stamps 1977b). For five species of Australian skinks it was found that males and females aggressively exclude other species from shelters when suitable habitat is limited (Langkilde and Shine 2004).

Nonadaptive Reasons for Female Aggression

Females may also be aggressive for nonadaptive reasons, such as a genetic correlation between the sexes (Rosvall 2011). In this scenario, aggression is a by-product of a shared genome with males, and may be heritable. For example, there is evidence in *Drosophila melanogaster* that male and female aggression is linked, because selection for male aggression concomitantly resulted in more aggressive females (Edwards et al. 2006). Given that females of many species have reduced color patches, similar to those of males, there is a possibility that aggressive behavior is likewise the product of a genetic correlation with males.

Aggression and Competition over Ecological Resources in Males

Ecological consequences of male aggressive behavior and agonistic interactions among individuals are context dependent. Variation in aggressive behavior in males is typically associated with dominance status, the ability to defend territories, and the concomitant exclusive access to resources. Yet, the outcome and function of aggression in males depends on prevailing population density, abundance and spatial dispersion of resources, variance in the operational sex ratio, and dispersal capacity (Zamudio and Sinervo 2003). Moreover, the levels of aggression among males may fluctuate with age (ontogeny) (Aragon et al. 2004). Inferences regarding the behavioral ecology of aggression in lizards require integration of intrinsic attributes of individuals, the social/demographic milieu, and the environmental context of social interactions.

Aggressive encounters between males are expected whenever there is intraspecific competition for limited resources. Ecological resources relevant to lizards include access to basking sites, food, retreat sites or refugia from predators, and acquisition of mates (Magnuson et al. 1979; Brattstrom 1974; Carpenter 1967). In some circumstances, as in moderately to relatively high densities, acquisition of resources (in this case females) enhances the dominance status of the individual. However, at low population densities or extremely high population densities, aggressive defense of a territory is not predicted to be favored by selection (Knell 2009).

Basking sites are a critical resource for lizards because body temperature affects physiological performance (Huey 1982). Variation in physiological performance is known to have fitness consequences (Miles 2004; Robson and Miles 2000; Huey 1991). For example, sprint speed is known to vary with temperature (Huey 1982), and faster lizards exhibit greater survival (Miles 2004). In addition, aggressive behavior is temperature sensitive (Mautz et al. 1992). For example, individuals of the Tussock Skink (*Pseudemoia entrecasteauxii*) with higher preferred body temperatures are also more aggressive (Stapley 2006). One outcome of male aggression is the acquisition of territories that incorporate preferred basking sites, resulting in lizards that attain high body temperatures and thereby maximize physiological performance (Calsbeek and Sinervo 2002b; Kondo and Downes 2007; Olsson and Shine 2000; Stamps 1977a). Indeed, many studies that estimate aggressive behavior in lizards focus on a basking site that serves as a resource to be competed for between males (Perry et al. 2004; Robson and Miles 2000). Thus, defense of territories with greater microhabitat complexity and more favorable basking sites is likely to affect a male's reproductive success via its ability to thermoregulate at a body temperature that maximizes its physiological performance. An observational study of the Eastern Fence Lizard (*Sceloporus undulatus*) found that aggressive displays were associated with basking sites (Haenel et al. 2003). Aggressive defense of space is also likely to result in males acquiring territories with higher perch sites which, in addition to enhancing

the detection of rivals (e.g., Andrews 1971) or promoting the effectiveness of signals (Tokarz 1985), may also provide enhanced opportunities for thermoregulation.

Aggressive behavior in males also has the key benefit of promoting the acquisition and defense of territories containing food resources, thereby enhancing their fitness (Stamps and Tollestrup 1984). Several studies have shown that territory size covaries with food availability (Adams 2001; Krekorian 1976; Simon 1975). Moreover, multiple studies have shown that dominant males settle in high quality territories (Calsbeek and Sinervo 2002b; Kohlsdorf et al. 2006). However, whether males are sequestering resource-rich space for their own energetic demands or to attract females (resource defense polygyny) requires experimental manipulation of food resources. For example, male Galápagos Land Iguanas (*Conolophus subcristatus*) appear, at least in part, to defend territories for access to food (Werner 1982), but an experimental manipulation of food availability (Christian and Tracy 1985) suggested that variation in territory size represented an interaction between the thermal quality of the habitat and its resource abundance.

Aggressive interactions may increase predation risk as a consequence of increased exposure during periods of activity. An additional benefit of aggressive behavior, however, is access to retreat sites. This benefits the animal by limiting its exposure to predators or by providing thermally beneficial shelter sites with warmer temperatures during periods of inactivity (Langkilde et al. 2005; Osterwalder et al. 2004). Experimental manipulations and field observations revealed that interspecific competition for preferred "warmer" refugia was intense among five species of skinks in the genera *Egernia* and *Eulamprus* (Langkilde and Shine 2004). The limited availability of preferred retreat sites, that is, warmer shelter sites or sites providing protection from predators, may result in dominant individuals that defend these from subordinates. Kohlsdorf et al. (2006) noted that dominant males of the Amazon Lava Lizard (*Tropidurus torquatus*) defended territories with more refuge sites than were present in lower quality territories. Additionally, dominant males had territories that overlapped with more females when compared to low quality territories. Additional results from experimental manipulations showed that dominant males of Leseuer's Velvet Gecko (*Amalosa* [=*Oedura*] *lesueurii*) excluded smaller, subordinate males from rocky retreat sites that were warmer and less likely to have been used by a snake predator (Downes and Shine 1998).

Sexual Selection

Male Aggression and Territorial Behavior

Aggression and territorial behavior are thought to influence mating opportunities and, more generally, reproductive success. A common pattern is that the mating success of males is linked with territory size and quality. Territory size serves to influence the number of female home ranges that a male's territory overlaps, whereas territory quality may be effective in inducing females to establish a home range adjacent to that of a dominant male. An observational and experimental approach by Hews (1990, 1993) demonstrated that males with a higher quality territory, as measured by food availability, led to greater mating success. Such studies support the hypothesis that food abundance in a male's territory determines, in part, mating opportunities and thus reproductive success (Kwiatkowski and Sullivan 2002). Removal experiments provide evidence that male defense of territories also entails the defense of potential mates. For *Urosaurus ornatus*, the removal of females from a male's territory resulted in the latter moving to a new location (M'Closkey et al. 1987b). In contrast, females did not alter their home ranges when the dominant male was removed. Multiple examples are available that demonstrate that male aggression and territorial behavior are linked with mate acquisition—Iguanidae: *Sauromalus obesus* (=*ater*) (Kwiatkowski and Sullivan 2002); *Ctenosaura hemilopha* (Carothers 1981); Phrynosomatidae: *U. ornatus* (M'Closkey et al. 1987a, b); *Sceloporus undulatus* (Haenel et al. 2003); Liolaemidae: *Liolaemus quilmes* (Robles and Halloy 2009); Crotaphytidae: *Crotaphytus collaris* (Husak et al. 2009); Lacertidae: *Iberolacerta cyreni* (Salvador et al. 2008).

Does Female Aggression Play a Role in Sexual Selection?

In order to understand the role of female aggression in sexual selection, it is useful to first clarify what we mean by sexual selection. We follow a broad definition, which is simply stated as "competition for mates" (Shuker 2010), as advocated by Rosvall (2011) for studies of intra-sexual selection. It therefore applies equally to both males and females.

Unfortunately, male lizards are far more likely to be the focus of studies of aggression and its role in sexual selection and social behavior than are females. This may, in part, be because males typically exhibit greater levels of aggressive intra-sexual competition and, as a consequence, agonistic display behavior, that they are more overtly territorial, and that they frequently have elaborate ornaments and armaments (Whiting et al. 2003; Kabelik et al. 2006; Stamps 1977b). These factors play into variance in reproductive success, which is typically greater in males, and explains why males are more likely to be ornamented (and aggressive) than are females (Rosvall 2011; Andersson 1994). There is also some debate, about animals more broadly, as to whether female aggression plays a significant role in sexual selection, as opposed to natural selection (Rosvall 2011; Clutton-Brock 2007). Furthermore, in addition to sexual selection, female traits may be the result of a genetic correlation, fecundity selection, or survival selection (the latter two cases being examples of natural selection).

The importance of female–female aggression more generally in animals has received increased attention in the past decade (Gill et al. 2007; Clutton-Brock and Huchard 2013; Clutton-Brock 2009; Rosvall 2013; Rosvall 2011), even if the study of lizards has lagged behind that of other taxa, such as mammals and birds, which exhibit more elaborate parental care. Nevertheless, females offer a rich avenue for research because there are numerous contexts in which we would expect females to be aggressive, and multiple hypotheses have been advanced to explain female–female competitive/aggressive behavior (Table 9.1). These are in dire need of testing. In some species, such as the Qinghai Toad-headed Agama (*Phrynocephalus vlangalli*), females appear to be as aggressive as males, and potentially even more so, because they are aggressive toward both males and females. Likewise, chameleons are renowned for their intolerance of conspecifics, and females of the Cape Dwarf Chameleon (*Bradypodion pumilum*) are highly aggressive toward courting males, commonly attacking and biting them. Larger female chameleons pose greater danger to courting males and, consequently, smaller females are more likely to be approached and courted by males (Stuart-Fox and Whiting 2005). The females of many lizard species, such as Yarrow's Spiny Lizard (*Sceloporus jarrovi*), are highly aggressive and territorial (Ruby 1978; Woodley and Moore 1999a; Sloan and Baird 1999; Stamps 1977b, a).

Females are also aggressive for reasons similar to those of males, including social and sexual selection. For example, if mate availability or male encounter rates are low, females are predicted to become more aggressive as they compete for males (in accordance with the mate limitation hypothesis). Furthermore, female aggression and competition are believed to be strongly influenced by male quality, as opposed to simply the number of available males (Rosvall 2011). For females, high quality males that provide direct or indirect (genetic) benefits may be a limiting resource, a factor that is often ignored in studies of both sexes (Rosvall 2011). To the best of our knowledge, the mate limitation hypothesis has only been tested for one species of lizard, the Qinghai Toad-headed Agama (*Phrynocephalus vlangalli*). This species exhibits male-biased dispersal, which potentially results in lower male availability. This could explain why females are particularly aggressive. In order to test the mate limitation hypothesis, sex ratios were manipulated in large outdoor enclosures under semi-natural conditions. Levels of female–female aggression were not, however, greater in enclosures with fewer males, refuting the hypothesis that female aggression is explained by lower male availability.

Female aggression has also been demonstrated to influence the mode of paternity acquisition (While et al. 2009a, b). In White's Rock Skink (*Liopholis* [=*Egernia*] *whitii*), females are consistently, but temporally, aggressive. Whereas female aggression was not influenced by density, body size, or territory size, more aggressive females were more likely to seek extra-pair copulations

Table 9.1 Hypotheses for Explaining Female Competition/Aggression

Hypothesis	Prediction	Plausible in Lizards?	Reference
Sexual Selection			
Competition for access to mates	Females more aggressive/competitive in female-biased OSR; potentially high numbers of receptive females and low numbers of available males	Yes, but has not been demonstrated	
Competition for access to high-quality mates	Females more aggressive/ competitive when male quality variable or males offer direct benefits. In case of territories, difficult to separate female preference for male or resources (territory)	Yes, but has not been demonstrated	
Competition for male parental care	Females compete if shared males result in reduced parental effort, reduced fitness; they compete to exclude rival females from males	Possibly in kin-based systems (e.g., *Egernia* group) if shared paternity reduces fitness of female's offspring	
Competition for indirect (genetic) benefits	Females compete for males based on genetic quality, e.g., leks	More aggressive female *Liopholis whitii* have more extra-pair offspring; may be better at securing high quality males	While et al. (2009a,b)
Competition for mating opportunities	Females competition/aggression increases with reduced access to mates and resources; e.g., females that control access to key resources may influence rival female RS	Unlikely, relies on females mostly or completely excluding rivals from access to males	
Sexual conflict	Females aggressively attack courting males they wish to avoid mating with	Yes, dwarf chameleons (*Bradypodion pumilum*) are highly aggressive toward courting males	Stuart-Fox and Whiting (2005)
Natural Selection			
Density	Female aggression will increase with density; stress levels will increase	Yes, may be confounded by competition over resources	
Food	Female aggression and food availability are inversely related	Yes, evidence in *Phrynocephalus vlangalii*	Wu, Whiting, Fu, Qi unpubl. data
Refugia	Female aggression will increase as refuge availability decreases	Yes, but has not been demonstrated	
Nests/eggs/offspring	Female aggression toward conspecifics increases in presence of eggs/offspring	Parental care in many *Egernia* group spp. through parent–offspring association reducing infanticide risk	Reviewed in Whiting and While (2017)
	Female aggression toward predators to protect eggs/offspring	Female *Eutropis longicaudata* will attack snakes to protect nests	Huang et al. (2013) and Pike et al. (2016)
Genetic correlation	Parent–offspring correlations in aggression, heritability	Yes, but has not been demonstrated	

Source: Modified from Rosvall (2011) and applied to lizards.

(Figure 9.1). It is not clear why females that are more aggressive are also more promiscuous. It may simply be a carryover from other traits (While et al. 2009a, b). For example, offspring of more aggressive females also exhibit higher first year survival (Sinn et al. 2008). Such outcomes are suggestive of the potential importance for female aggression on fitness and highlight the need to look beyond male aggression in studies of sociality and reproductive fitness.

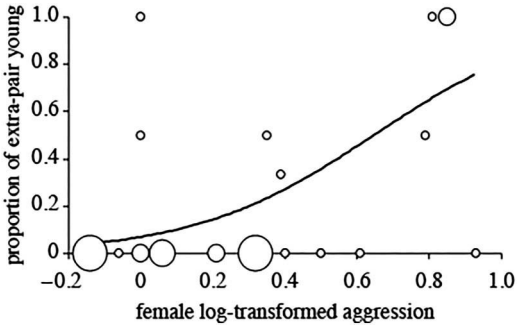

Figure 9.1 The relationship between female aggression and the likelihood of extra-pair paternity in the family-living White's Rock Skink (*Liopholis whitii*). More aggressive females sired a higher proportion of extra-pair offspring. Circle size sample size where the smallest dot 1 and the largest 4. (Figure reprinted from While et al. 2009a, b.)

Aggression and Alternative Mating Strategies

Competition for mates among males is often intense and involves a diverse array of behaviors for ensuring reproductive success. Differences in competitive abilities or aggression, such that asymmetries in reproductive opportunity among males become established and favor the evolution of alternative mating strategies (AMSs) (Maynard Smith 1974). Thus, males adopt divergent behavioral strategies, which enhance mating opportunities. Factors promoting variance among males in reproductive success include size hierarchies or dominance hierarchies, where only large or dominant males can acquire territories and mates to the exclusion of smaller, less aggressive males.

Alternative mating strategies may be fixed throughout life, or they may be labile (Noble et al. 2013). The former often have a genetic or developmental basis for a polymorphism in male mating tactics. In contrast, the labile polymorphisms in mating tactics may be condition dependent, facultative or plastic (Zamudio and Sinervo 2003). In some species, there may be a morph that switches from one tactic to another during ontogeny and changes in social context (Sinervo et al. 2000). Examples of the genetic basis of alternative reproductive tactics include the fixed color polymorphisms of males (e.g., *Uta stansburiana*, *Urosaurus ornatus*, *Sceloporus grammicus*). Condition-dependent alternative reproductive strategies include those relating to body size (*Amblyrhynchus cristatus*, *Iguana iguana*), variation in head size and dewlap size (*Anolis carolinensis*), and variation in coloration, for example, *Chlamydosaurus kingii* (Merkling et al. 2016), *Lacerta agilis* (Molnár et al. 2016), and *Iberolacerta* (=*Lacerta*) *monticola* (Aragon et al. 2004).

Although fixed and labile AMSs result in asymmetries of resource-holding potential and reproductive opportunities, the conditions for the evolution of each type differ (Sinervo and Calsbeek 2006; Miles et al. 2007). In the former, fitness advantages of one morph will ultimately lead to the elimination of other morphs through natural selection (Zamudio and Sinervo 2003). However, if the fitness of one strategy varies according to the frequency of alternative strategies, then multiple morphs may be maintained by negative frequency-dependent selection (Sinervo and Zamudio 2001; Sinervo and Calsbeek 2006; Miles et al. 2007). That is, a specific reproductive tactic will have a fitness advantage when rare. Labile alternative strategies should be maintained when the benefit of pursuing a dominant strategy exceeds its cost (Zamudio and Sinervo 2003). Alternative mating strategies may involve two or more patterns of morphological and behavioral traits among males that are linked with differences in resource holding potential (RHP). A notable feature of AMSs is the variation in energy apportioned into reproductive behavior and competition among the male morphs (Taborsky and Brockmann 2010; Zamudio and Sinervo 2000). In a typical AMS system, a dominant male (also known as a bourgeois male) exhibits high levels of aggression and defends

a large territory that overlaps with those of multiple females, leading to higher reproductive success and greater resource-holding potential. Variation in the density of dominant males dictates the magnitude of individual interactions and the strength of competition for mates. Monopolization of space by dominant males generates copulation opportunities for subordinate males (Taborsky and Brockmann 2010) (also sometimes called satellite, floater, or sneaker males), which are either not capable of defending territories or unable to usurp space from a resident in an existing territory (Baird et al. 1996). As a consequence, these subordinates exhibit subdued coloration to avoid agonistic interactions with dominant males and rarely engage in aggressive interactions. Reproductive opportunities are obtained by satellite males through parasitizing copulations with females defended by the dominant male or by sneaker males having phenotypic traits that mimic those of females (Sinervo and Lively 1996; Sinervo et al. 2000; Zamudio and Sinervo 2000, 2003; Wikelski et al. 2005).

Aggression within Genetic and Developmentally Determined AMSs

The alternative mating strategies displayed by a population of *Uta stansburiana* in the Coast Range of California at Los Baños has been the focus of an intensive long-term study. Males in this population occur at high densities on isolated rocky outcrops. Sinervo and Lively (1996) documented a complex mating system involving three male color morphs. Two of these defend territories using different behavioral strategies (Calsbeek et al. 2002). Ultra-dominant, aggressive orange-throated males (hereafter referred to as orange males) have high resource usurping potential that is based on their extreme fighting ability. Usurpation is a risky strategy that may not result in any mating opportunities (Calsbeek et al. 2002). The aggressive behaviors shown by orange males are associated with high levels of testosterone (Zamudio and Sinervo 2000) and result in the defense of large territories situated in high-quality thermal environments that overlap with those of multiple females (Calsbeek and Sinervo 2002a). However, orange males, owing to their larger territories, are unable to repel the sneaker yellow-throated males (hereafter referred to as yellow males). Blue-throated males (hereafter referred to as blue males) defend smaller territories that overlap with fewer females. Blue males exhibit a mate-guarding strategy and engage in cooperative behavior with other blue males to repel sneaker males (Sinervo et al. 2006). As a result, blue males prevent other males from copulating with their females, but this also reduces opportunities for additional copulations. Among the territorial males, territory size is significantly and positively correlated with the number of overlapping female home ranges. Yellow males adopt a non-territorial, sneaker strategy and remain on the periphery of the ranges of territorial males, using female mimicry to avoid agonistic interactions with dominant males (Zamudio and Sinervo 2003). Mimicking females also allows yellow morph males to sneak copulations without detection by orange males.

Another species, *Urosaurus ornatus*, exhibits a similar pattern of throat color polymorphism in males, yet differs in the behavioral strategies associated with each morph. In many populations of *U. ornatus*, males are characterized by a discrete throat color polymorphism consisting of three hues: orange, yellow, and blue (Figure 9.2; Thompson and Moore 1991; Lattanzio and Miles 2016; Miles unpublished). A few populations have at least six morphs that co-occur in a population, characterized by the three colors and their combinations, for example, orange-blue, yellow-blue, and orange-yellow (Thompson and Moore 1991). The morphs differ in resource-holding potential and levels of aggression. Blue males, including orange-blue and yellow-blue morphs, defend territories (Lattanzio and Miles 2014; Miles unpublished). Yellow males behave as satellites and are affiliated with dominant males, but do not defend territories (Miles unpublished). Orange males are nomadic (Hews et al. 1994). However, whether a male engages in satellite or nomadic behavior depends on the environmental conditions prevailing during ontogeny (Knapp et al. 2003). One intriguing aspect of the mating system of *U. ornatus* is the prevalence of geographic variation in the number of morphs within a population and in morph frequency (see Figure 9.2; Hews et al. 1997). Despite

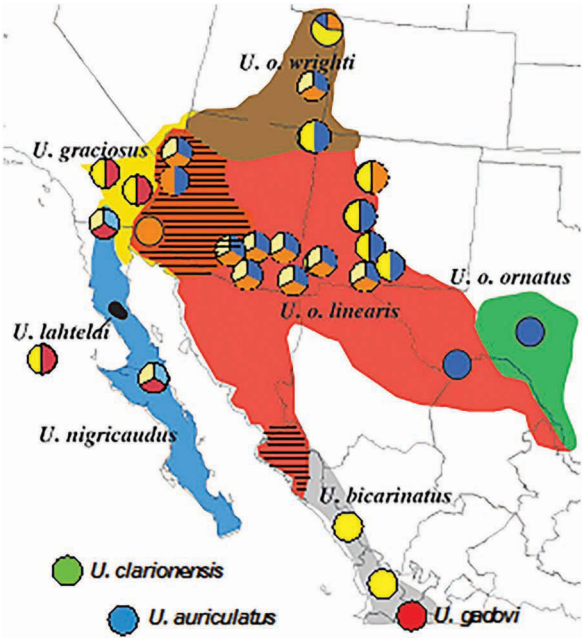

Figure 9.2 Geographic variation in morph frequencies among populations and subspecies of *Urosaurus ornatus*. We provide morph data for seven additional species, including two species on islands (*U. clarionensis* and *U. auriculatus*). Trimorphic color patterns have evolved independently in *U. nigricaudus* (=*microscutatus*) and *U. ornatus* based on ancestor reconstructions (Feldman et al. 2011). Substantial variation in morph frequencies within *U. ornatus* is evident. Circles portray the number of morphs found in each population. Circles with a single color are monomorphic, with two colors dimorphic and three colors trimorphic. Colors in each circle indicate the morphs found at each population. (Data from Miles (unpublished).)

the pronounced among population variation in the number of morphs, data on aggressive behavior is available for only a few populations.

The Tawny Crevice-dragon (*Ctenophorus decresii*), in some parts of its range, is also characterized by discrete polymorphism consisting of four morphs: orange, orange-yellow, yellow, and gray (Yewers et al. 2016). Orange morphs are the most aggressive, yellow or yellow-orange morphs exhibit intermediate levels of aggression, whereas gray morphs exhibit the least aggression. Variation among the morphs has a genetic basis and can be described by a model with two autosomal loci (Rankin et al. 2016). Orange and yellow morphs also have high heritabilities. The behavioral strategy of yellow morphs (either orange-yellow or yellow) is contingent on the morph of the intruder. Yellow males display more aggressively toward yellow and orange intruders, but show lower levels of aggression to a gray morph intruder. In addition, experimental studies have shown that males recognize intruders based on throat color (Osborne et al. 2012). Thus, *C. decresii* exhibits a male morph-specific reproductive strategy that comprises ultra-dominant males (orange), satellite males (gray), and a morph (yellow or yellow-orange) with plastic strategy depending on the social context.

Condition-Dependent AMSs

In mating systems characterized by condition-dependent AMSs, males may exhibit labile or plastic aggressive responses to conspecifics. Thus, males may switch from a territorial, satellite, or sneaker strategy to another contingent on the social and environmental context. Two key attributes

that determine whether males will transition to a new mating strategy are population structure and availability of territories. Transitioning from a satellite to territorial male depends on the relative density of dominant, territorial males. If few large males are present in the population and sufficient resources/space is available for defending a territory, a male may shift to a new mating strategy. Whether a male adopts a territorial strategy also depends on the age and size of the individual. Larger, older males are more likely to have high resource-holding potential compared to younger, smaller males.

The mating behavior of the Marine Iguana (*Amblyrhynchus cristatus*) provides an example of a labile AMS. Marine iguanas engage in reproductive activities along the coastline that consists of sandy beaches and rocky outcrops. In these habitats, numbers of marine iguanas in local aggregations can be high (e.g., >2,000 individuals on one beach on Isla Genovesa; Wikelski et al. 2005). Three male reproductive phenotypes are present in such a population: territorials, satellites, and sneakers (female mimics). Young males that are smaller tend to adopt the sneaker reproductive phenotype. They resemble females in both size and behavior, yet are reproductively mature (Wikelski et al. 1996). Territorial males cannot discriminate between sneaker males and females, resulting in sneaker males not being harassed when they intrude into a territory. Sneakers attempt copulations when a male is away from his territory. Larger, older territorial males aggressively defend small territories, signaling their status using head-bobbing (Partecke et al. 2002). Satellite males are intermediate in size, have larger heads than sneaker males, elongated dorsal spines, and assume the male breeding coloration. Territorial males engage in agonistic interactions in an attempt to exclude satellite males from their territory. Satellite males, however, move through territorial interstices and will pursue females (Partecke et al. 2002). The territorial status of males is dynamic. Some will expel a holder, thereby usurping adjacent territories. Satellite males can transition to the territorial phenotype depending on their age and the availability of suitable territories. Transitions in territorial status are modulated by testosterone (*T*) (Wikelski et al. 2005). Males implanted with *T* exhibited higher rates of head-bobbing, but males implanted with a testosterone antagonist exhibited lower rates of head-bobbing and a concomitant reduction in territory size. The aggressive behaviors of males are mediated by the demographic milieu (that is, the density of older and larger males), and appropriate conditions trigger a surge in *T* production and leads to a shift in dominance status and, therefore, reproductive phenotype, of satellite males.

Size- and age-related variation in aggression is a characteristic of the Eastern Water Dragon (*Intellagama* [=*Physignathus*] *lesueurii*). Males exhibit two reproductive tactics. Dominant, territorial males are larger than members of a second group, non-territorial satellite males, and frequently patrol territories (Baird et al. 2012). Experimental removal of large, dominant males resulted in the transition in mating tactics of large satellite males from non-territorial to territorial (Baird et al. 2012), this being accompanied by a transition in aggressive behaviors on the part of the winning male.

In general, most labile AMSs entail transitions in mating tactics as a consequence of size and age (Baird et al. 1996; Baird and Sloan 2003; Baird 2013). A shift in aggressive status may also be accompanied by a transition in coloration. Males of the Iberian rock lizard (*Lacerta monticola*=*Iberolacerta cyreni*) have two reproductive phenotypes. Younger, smaller males are dull brown in color and resemble females, whereas older, larger males are green. Green males display more frequently and become engaged in more conspicuous agonistic interactions than brown males (Aragon et al. 2004).

An unresolved question in the study of AMSs is whether a male adopting an aggressive strategy always enhances its mating opportunities. Variation in male behavioral morphs in the monogamous Sleepy Lizards (*Tiliqua rugosa*) can be used to address this question. Males of this species exhibit variation in their level of aggressiveness, but can be placed into one of two behavioral types (Godfrey et al. 2012). "Fighters" exhibit high levels of aggressive behavior (based on behavioral assays) as well as sporting wounds acquired during fights with other males. "Lovers," in contrast, display

lower levels of aggressiveness. A social network analysis revealed that less aggressive "lovers" had more frequent associations with females. In contrast, highly aggressive "fighters" showed limited associations with females and often remained unpaired (Godfrey et al. 2012). In this species at least, aggressiveness results in lower opportunities for mating.

Aggression without Territoriality—Mate Guarding

Rather than using aggression to enhance fitness indirectly by defending territories, males may defend females. Species in the family Teiidae are active foragers whose home ranges are correlated with body size and energy requirements (Pianka and Vitt 2003). Although both male and female teiids exhibit aggressive behaviors, they do not defend territories (Winck et al. 2011). For example, the home ranges of male Anguilla Bank Ameivas (*Pholidoscelis* [=*Ameiva*] *plei*) exhibit substantial overlap (Censky 1995). The number of females overlapping with a male's home range was positively correlated with home range area. Most agonistic encounters between males appear to be directed at access to females, and larger males won the majority of intra-sexual contests. In addition, most copulations were co-opted by a small number of males. After mating, males remain with females during the first days of receptivity. The role of aggression in the absence of territorial behavior in *P. plei* appears to be related to the acquisition of females and subsequent mate guarding after copulation. The large home ranges of teiids prevent males from defending females from other males. Hence, higher reproductive success in non-territorial males, at least in teiids, is accomplished initially through aggressive behavior by larger males allowing them to gain access to females, followed by mate guarding. Mate guarding has also been documented in European Sand Lizards (*Lacerta agilis*) where larger males defend females for longer periods of time. Males are also more likely to mate-guard females of similar age to themselves. However, the amount of time a male guarded a female was unrelated to the female's body size (Olsson et al. 1996).

Aggression and Fitness

The link between aggression and fitness is largely unexplored because few studies focus explicitly on long-term aggressive behavior and how this may influence fitness. Aggression, however, is linked to many factors, such as AMS, that may covary over a season or lifetime, allowing us to draw some inferences about this relationship. For example, male Collared Lizards (*Crotaphytus collaris*) with high scores for aggression spent more time courting females (Baird et al. 2007). Paternity analyses have shown a significant link between aggression, social status, and reproductive success (Lebas 2001; Baird et al. 2007; Stapley and Keogh 2006; Husak et al. 2009). In many of the species that have been examined, larger, dominant males of high social status also attained high reproductive success. Larger, dominant males of the Common Puerto Rican Ameiva (*Pholidoscelis* [=*Ameiva*] *exsul*) sired more offspring than did smaller or lower status males (Lewis et al. 2000). Male *Iberolacerta cyreni* that exhibit higher activity levels, which is associated with dominance, sired the most offspring (Salvador et al. 2008). Interestingly, the same males also have higher survivorship to the next year.

As mentioned previously, more aggressive females of *Liopholis whitii* were more likely to seek extra-pair matings and this may well have positively impacted their fitness. To determine whether this is the case, however, long-term monitoring of their offspring would be needed. For this species, males that were assayed for aggression and followed in the field for a season did not sire more offspring, and their body size and its relationship to aggression was found to be unrelated to reproductive success. Finally, the territories of the more aggressive individuals did not overlap with those of more females, nor did they maintain larger home ranges (McEvoy et al. 2012). In the case of the Side-blotched Lizard (*Uta stansburiana*), the fitness of the most aggressive morph (orange) is frequency dependent, and therefore, its behavioral type is less important. That is, the fitness payoff

for orange males is contingent upon the frequencies of the alternative morphs. In particular, yellow males parasitize copulations from females overlapping an orange male's territory. A complicating factor is that yellow males sire more offspring posthumously. As a consequence, sperm storage by females may have a major effect on the fitness of each morph (Zamudio and Sinervo 2000). A similar pattern was found for the Painted Dragon (*Ctenophorus pictus*). Red males are aggressive and dominate yellow males (Healey et al. 2007), and emerge earlier. However, yellow males are sneakers and have larger testes (Olsson et al. 2009). Although red males are the dominant, aggressive morph and copulate with females for longer, yellow males sire more offspring (Olsson et al. 2009).

Social Selection

Maternal Aggression and the Potential Benefits to Offspring

Female aggression in lizards, particularly in the context of reproduction, is often linked to season and reproductive state. For example, females may become more aggressive during pregnancy or during the postpartum period (Sinn et al. 2008). If females are most aggressive during pregnancy, this may be a by-product of changing hormonal profiles or may be a strategy for maintaining an exclusive area for the benefit of their offspring. Likewise, female postpartum aggression could be adaptive if offspring gain from reduced competition with nonkin. In the case of egg-laying species, aggression in postpartum females may be a consequence of nest site defense. Although aggression *per se* was not the focus of research on the Long-tailed Sun Skink (*Eutropis longicaudata*), it was found that females aggressively protect their nests from egg-eating snakes (Huang 2006; Pike et al. 2016) on Orchid Island (Taiwan). Adults are too big to be preyed upon by sympatric snakes and are able to protect their nests by directly attacking foraging snakes. In the Collared Lizard (*Crotaphytus collaris*), nest defense was excluded as accounting for postpartum female aggression, with the most likely explanation being that aggression helps females reestablish residency after leaving their territories for several days to lay their eggs (Sloan and Baird 1999). Nest defense and egg brooding has been documented for a variety of lizards (approximately 60 species, 12 families) and is most common among scincid lizards (Somma 2003; While et al. 2009a, b; Noble and Mason 1933). In the case of the Five-lined Skink (*Pleistodon* [=*Eumeces*] *fasciatus*), females aggressively defend their eggs against attack by predators (Noble and Mason 1933). In one instance, a Northern Prairie Skink (*Plestiodon* [=*Eumeces*] *septentrionalis*) attacked and killed a ringneck snake (*Diadophis punctatus*) introduced into its enclosure where it was brooding a clutch of eggs (Somma 1985).

In the *Egernia* group of lizards, parental presence, and by extension aggression, may well have influenced the evolution of parental care (Chapter 10). Females are viviparous and the offspring of many species exhibit delayed dispersal and live in family groups. If they disperse too soon, they risk infanticide by unrelated adults. By associating with their parents at a time when they are most vulnerable, the risk of attack by an unrelated adult is almost eliminated (While et al. 2014; Whiting and While 2017). This has been experimentally demonstrated for the Black Crevice Skink (*Egernia saxatilis*) (O'Connor and Shine 2004). Furthermore, both *E. saxatilis* and *Liopholis whitii* display heightened female postpartum aggression (O'Connor and Shine 2004; Sinn et al. 2008), and in the case of *L. whitii*, females are twice as aggressive during and after pregnancy than they are during nonreproductive periods. Furthermore, female aggression toward conspecifics is a predictor of offspring survival in this species (Sinn et al. 2008). There is also the possibility that female and/or male parental aggression may impact offspring survival directly. An adult King's Skink (*Egernia kingii*), in the presence of its offspring, attacked and chased an approaching predatory Tiger Snake (*Notechis scutatus*) (Masters and Shine 2003). Although this is only a single observation, it certainly warrants more experimental follow-up in family-living species. In many *Egernia* group species, lizards are confined to discrete habitat patches, such as rock outcrops, where they seek refuge

in crevices. This results in increased competition and greater potential for aggressive encounters with unrelated conspecifics. By delaying dispersal to avoid the costs of aggressive encounters, the stage is set for the evolution of kin-based sociality (Chapter 10) (While et al. 2014; Whiting and While 2017; While et al. 2009a, b).

Patterns of Social Organization in Lizards—Dominance Hierarchies, Hotshots, and Despots

A major outcome of aggressive behavior is the establishment of social structure in lizards (Carpenter 1967). The type of social structure depends on how individual males differ in their range of assertion displays or intensity of agonistic interactions. Research has demonstrated a positive association between elaborate aggressive displays and complex social structure (Carpenter 1967; Radder et al. 2006a, b). Furthermore, species with greater degrees of expression of sexual dimorphism, as a consequence of high population density and intense contest competition, exhibit more elaborate displays (Ord et al. 2001). Differences in social structure may vary among populations depending on a variety of factors. A primary factor is the role that population density and intensity of intraspecific competition plays. A second factor is the dispersal capacity of individuals, that is, the potential of an individual to change neighborhoods and exploit different social contexts. A third factor involves elements of the habitat, such as habitat type, habitat complexity, resource availability, and dispersion. These latter attributes dictate the heterogeneity of the environment. A habitat with high heterogeneity provides the opportunity for males to defend and monopolize resources. In contrast, homogeneous environments and even distribution of resources may prove to be difficult circumstances for males to defend territories.

In most lizard species, social organization may be rigid and not vary within a season. In contrast, social organization may be transient and become modified as conditions change, such as during drought versus wet conditions, or if a dominant individual or a territorial resident dies. Moreover, social structure varies according to the mating system of the species (Brattstrom 1974). Aggressive and agonistic behaviors in males are often linked with territorial defense that excludes intruders from access to resources. Males of *Iberolacerta cyreni* have a large home range, but a smaller core area is defended from other males (Aragon et al. 2004). Depending on the prevailing circumstances, social structure in lizards may depart from a territorial organization to a dominance hierarchy, leks, or despotic structure.

Dominance Hierarchies

Dominance hierarchies are expected to emerge in three circumstances. First, high population densities result in increased frequencies of aggressive interactions (Alberts 1994; Brattstrom 1974). This may elevate the cost of defending territories and exceed the realized benefits for either food resources or mating opportunities (Kwiatkowski and Sullivan 2002). In addition, constraints on dispersal favor the development of a dominance hierarchy. Second, if the operational sex ratio is skewed toward females, males are expected to compete for females and, as a consequence, a dominance hierarchy often emerges to enhance harem defense (Carothers 1981). Third, spatially dispersed resources will also facilitate the development of a social hierarchy (Stamps 1977a). At extremely high densities, males are predicted to form leks (Kwiatkowski and Sullivan 2002).

Most dominance hierarchies are based on body size, as in the Six-lined Racerunner (*Aspidoscelis* [=*Cnemidophorus*] *sexlineatus*), where captive males form a linear dominance hierarchy structured by an interaction between body size and aggressive behavior (Brackin 1978). The Cuban Iguana (*Cyclura nubila*) forms dominance hierarchies based on body size, head width, femoral pore size, and display rates. High-ranking, aggressive males are larger; have relatively larger jaw musculature; possess enlarged femoral glands; and have larger home ranges (Alberts et al. 2002). Low- and

non-ranking males are smaller in size, exhibit lower display rates, and have smaller home ranges. The largest proportion of dominance displays and courtship attempts occur among the largest, highest ranked males. A removal experiment revealed that low ranking males could occupy an abandoned dominant male's home range. Thus, the larger, dominant males preclude low ranking males from occupying territories. Although a hierarchical structure characterizes the social system of *C. nubila*, Alberts et al. (2002) classified males into dominant, territorial individuals; non-territorial satellite individuals; and pseudofemale/sneaker individuals based on morphological and behavioral variables (see also Wikelski et al. 1996). In the absence of paternity data, the mating success of these social classes may be hypothesized to represent alternative strategies for mating opportunities.

Competition for spatially dispersed and limiting resources (coarse-grained environment) is the likely mechanism that explains the emergence of dominance hierarchies in the dune-inhabiting Desert Plated Lizard (*Gerrhosaurus* [=*Angolosaurus*] *skoogi*) in the northern Namib Desert. Males defend territories centered on the sparsely distributed plant species nara (*Acanthosicyos horrida*) (Pietruszka 1988). The dominance hierarchy of *G. skoogi* results from the defense of nara plants. Larger and darker colored males aggressively exclude smaller males from the vicinity of the plants. Dominance hierarchies may also characterize non-territorial species. Species in the family Teiidae typically do not defend territories (Stamps 1977b), but agonistic interactions among individuals are structured by body size. Larger individuals of *Pholidoscelis exsul* display a size-based dominance hierarchy. Male–male aggressive interactions are likely to center on access to optimal basking and foraging sites (Lewis et al. 2000). An alternative hypothesis is that the size hierarchy among male *P. exsul* enhances mating opportunities for larger males, which patrol larger home ranges (Lewis and Saliva 1987). Dominance hierarchies also emerge in species when held in captivity.

Leks and Hotshots

Marine Iguanas (*Amblyrhynchus cristatus*) form large aggregations on the rocky coastline of the Galápagos Islands and males defend small territories for attracting females within the aggregation during the reproductive season. This pattern of defending a territory for mating opportunities (non-resource based) among a cluster of males meets the definition of a lek. Wikelski and colleagues described the mating system and dominance behaviors in a series of papers (Partecke et al. 2002; Vitousek et al. 2008; Wikelski et al. 1996; Wikelski et al. 2005). Larger males occur within the core area of the lek (Wikelski et al. 1996), but the locations of the leks do not depend on female density (Partecke et al. 2002). Observational data show that males coalesce around large males with established territories. Two explanations for the lekking behavior, that is, clustering of territories, of marine iguanas have been proposed. First, males aggregate around areas that support high densities of females (hotspot model). Second, males selectively settle near males that are attractive to females (hotshot model). These core males exclude subordinate males and are also more frequently visited by females, supporting the hotshot hypothesis (Partecke et al. 2002).

Despotic Social Systems

In contrast to hierarchies, in which dominance status is arrayed in a linear order, there are social systems in which a few dominant individuals defend territories and the remaining, coexisting males hold subordinate, non-territorial status. These latter individuals may be satellite, nomadic, or floater males. The domination of other males by a few aggressive individuals is characterized as a despotic social system (Carpenter 1967). Despotic behavior is usually observed in territorial lizards for which there is extreme competition for space. Despotic social behavior has been observed in a variety of species: *Urosaurus ornatus* (Deslippe et al. 1990), *Microlophus* (=*Tropidurus*) (Carpenter 1966b), *Plica plica* (Debusk and Glidewell 1972), *Crotaphytus collaris, Uta stansburiana* (Calsbeek and

Sinervo 2002b), *Sauromalus ater* (=*obesus*) (Prieto and Ryan 1978), and *Lampropholis guichenoti* (Torr and Shine 1996). In each instance, despotic behavior is also observed in lizards maintained in captivity.

PART IV: CONSEQUENCES OF AGGRESSION FOR THE EVOLUTIONARY AND ECOLOGICAL TRAJECTORY OF POPULATIONS

An underappreciated aspect of aggressive behavior is the population consequences that result from agonistic interactions. When resources are limiting, individuals may acquire exclusive access to these resources by aggressively defending space to exclude other individuals. Because the number of territories that may be supported in an environment may be less than the number of mature males, the opportunities for reproduction may be limited. Hence, territoriality is often regarded as a mechanism of density-dependent regulation (López-Sepulcre and Hanna 2005; Philibosian 1975; Stamps and Tollestrup 1984). Two facets are, however, ignored in this conclusion. First, individual variation in resource-holding potential is ignored. Second, species that exhibit alternative mating strategies are composed of individuals with divergent behavioral repertoires. High variation in reproductive success may enhance demographic stochasticity (especially in small populations) that may increase temporal variation in population size (López-Sepulcre and Hanna 2005; Calsbeek et al. 2002). Complex dynamic behaviors are likely to arise depending on fecundity levels (low vs. high), territory size, and the cost of territorial defense (López-Sepulcre and Hanna 2005). In contrast, other studies have suggested that alternative mating systems stabilize social systems (Bastiaans et al. 2013; Aragon et al. 2004). Here, we consider four population consequences of aggressive behavior. First, we consider how individual variation in aggression associated with throat color polymorphisms results in trophic polymorphism. Second, we consider how AMSs generate demographic stochasticity, but potentially moderate the risk of population extinction in species with low density. Third, we show how intrasexual and intersexual aggression may be altered by anthropogenic environmental change. Finally, we discuss an example of how intersexual aggression may affect reproductive success and reduce population growth rates, leading to population collapse.

Aggression, Color Morphs, and Trophic Polymorphisms

In nearly all studies of AMSs, it is assumed that each morph, despite showing differences in behavior, morphology, physiology and life history characteristics, have few if any differences in other ecological characteristics. For example, no differences in the use of microhabitat among morphs could be detected in the Tawny Crevice-dragon (*Ctenophorus decresii*) (Teasdale et al. 2013) or diet in the Dalmatian Wall Lizard (*Podarcis melisellensis*) (Huyghe et al. 2007). In contrast, males of *Urosaurus ornatus* differ in microhabitat use and diet (Lattanzio and Miles 2016). Agonistic behavior by dominant blue males resulted in microhabitat segregation. Dominant males settled in high-quality territories (live oak trees) with abundant prey, whereas satellite yellow males and nomadic orange males often settled on lower quality habitats (snags) that had lower resource abundance (Lattanzio and Miles 2014). An analysis of dietary patterns using stable isotopes revealed segregation among morphs in the trophic level of their prey base. Blue males fed on prey higher in the trophic web than yellow or orange males (Lattanzio and Miles 2016). Patterns of dietary divergence among morphs also exhibited variation due to habitat disturbance. At high disturbance sites, yellow males converged on the diet of blue males. Orange males in both habitat types consumed a high proportion of either C_3 or C_4 herbivores (Figure 9.3). The pattern of diet niche segregation among the morphs was taken as evidence that an interaction between socially mediated sexual selection and natural selection exists.

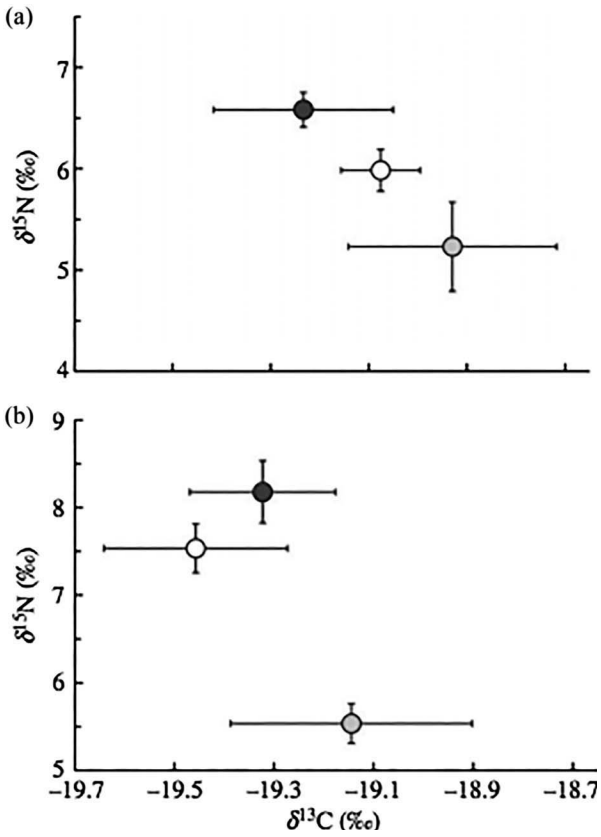

Figure 9.3 Trophic niche differences among male *U. ornatus* color morphs. Trophic relationships at (a) low-frequency burn and (b) high-frequency burn sites. Points are mean δ^{13}C and δ^{15}N values. Symbols designate different male color morphs: yellow (light gray), orange (gray), or blue (dark gray). Bars represent ±1 standard error ($n \geq 3$ for each group). (From Lattanzio and Miles 2014.)

Alternative Mating Strategies and Demographic Stochasticity

A characteristic of alternative mating strategies is the unequal fitness among the different behavioral phenotypes. The persistence of morphs within a population is accomplished through the intransitive nature of the fitness differences. One aspect of the AMS in *Uta stansburiana* is the cyclic behavior of the morph frequencies (Sinervo and Lively 1996). During any phase of a cycle, one of the three morphs will be rare. As a consequence, the rare morph is anticipated to exhibit higher reproductive success due to uncertainty in mating opportunities. Consequently, the long-term geometric mean fitness is equal among the morphs (Calsbeek et al. 2002). However, a key question is how do morphs with unequal fitness persist within a population? The two territorial morphs of *U. stansburiana* (orange and blue, see above) use alternative methods for acquiring and defending resources (Calsbeek et al. 2002). Ultra-dominant orange males usurp space whereas blue males are resource defenders. The former mating strategy has associated costs acting through the risk of low reproductive payoff. Paternity analyses have revealed that the usurper strategy has a mean fitness greater than the defender strategy, but with a higher variance in reproductive success. That is, usurpers experience extreme variability in the number of progeny sired; some males sire many offspring whereas many males sire none. The variation in fitness promotes the coexistence

of the two morphs through demographic stochasticity, that is, random variation in either survival or reproduction. This scenario arises because the higher variance in the usurper strategy results in lower geometric mean fitness among generations and approaches the fitness of the defender strategy. Potential fluctuations in population size arising from differences in the reproductive success of each strategy are minimized by the influence of demographic stochasticity.

Alteration of Intrasexual and Intersexual Aggression by Anthropogenic Effects

Human-induced changes in global environments are resulting in rapid loss of habitat, increased fragmentation of remaining habitat, and a warmer planet. These anthropogenic threats have the potential to drive alterations in aggressive interactions and the structure of lizard social systems. At one extreme, alteration of available thermal niches through global warming and habitat modification (e.g., drought) is predicted to result in local extinction of populations by diminishing hours of activity (Sinervo et al. 2010). Many populations may occupy habitats that are shared with humans. The loss of available habitat to support populations along with increasing interactions with human activity is likely to result in higher local densities and increased agonistic interactions among individuals. A comparison of the Cuban Rock Iguana (*Cyclura nubila*) inhabiting sites with high anthropogenic activity and those from a site with low activity revealed differences in aggressive behavior and social interactions (Lacy and Martins 2003). Iguanas that occupy sites with high human activity exhibit higher densities (perhaps due to human trophic subsidies (Jessop et al. 2012)) and altered behavioral interactions. Male–male social interactions increased in frequency and included more intense aggressive behaviors. Furthermore, male–female interactions diminished. Overall, human activity resulted in a significant shift in the social organization of rock iguanas. Alterations of intra- and intersexual interactions may have demographic consequences that include lower reproductive output and diminished survival of juveniles and adults.

Intersexual Aggression May Affect Reproductive Success and Lead to Population Collapse

The population ramifications of intersexual aggression have received scant attention in the literature (see Rankin and Kokko 2006). Sexual conflict is likely to perturb population dynamics because of the divergent behavioral roles of males and females during mating and reproduction (Arnqvist and Rowe 2005). In some species, mating behavior of males involves aggression and intimidation of females. For example, aggressive mating behavior in the European Common Lizard (*Zootoca* [=*Lacerta*] *vivipara*) involves coercion (prolonged courtship), multiple mating attempts and copulation (biting of females by males, D.B. Miles pers obs.) (Le Galliard et al. 2008). Thus, mating can result in injury or harm to females as a result of the aggressive behavior of courting males. Potential fitness costs of male aggressive behavior could include a reduction of female survival or lower reproductive output. Le Galliard et al. (2005) manipulated the sex ratio in a series of seminatural population enclosures. The adult sex ratio was skewed toward either females or males. Their results revealed that females in male-biased treatments carried more mating scars, suggestive of multiple male copulations and lower reproductive success (Fitze et al. 2005). In addition, survival probabilities of females decreased, as did fecundity (Le Galliard et al. 2005). Long-term monitoring of the experimental populations has revealed a rapid decline in abundance of lizards in the male-biased treatments (Le Galliard et al. 2005). Local extinction of a population was a consequence of lower lifetime reproductive success of females (Le Galliard et al. 2008), illustrating the population consequences that occur when highly aggressive male behavior incurs a major fitness cost for females.

FUTURE DIRECTIONS AND LIZARDS AS A MODEL SYSTEM FOR STUDIES OF AGGRESSION

Our chapter demonstrates the versatility of lizards as a model system for the study of aggressive behavior and its consequences for our understanding of social systems, population structure, and ultimately, fitness. Lizards, by virtue of the ease with which they can be studied, constitute an excellent system for behavioral and evolutionary ecological studies. They are mostly easily observed and habituate to the presence of an observer. They also have an extensive repertoire of dynamic and static signals and the outcome of a contest is normally unambiguous. Furthermore, endocrine and genetic studies have helped uncover the expression of alternate phenotypes linked to reproductive tactics that express differing levels of aggression. Indeed, studies of individual variation in behavior demonstrate consistent differences in behavioral types (i.e., personality) in many species. What is less clear is whether these behavioral types are fixed over an individual's lifetime and whether there is a trade-off between reproductive success and survival. For example, do more aggressive individuals attain more copulations in a single season, but have lower survival because of the physiological costs of aggressive behavior? We need to know more about both the long-term costs and fitness consequences of aggression. A particularly interesting phenomenon to emerge as a result of recent research on lizards is the existence of sibling rivalry in family-living lizards of the *Egernia* group (While et al. 2014; Riley et al. 2017). This is well known in birds and mammals, but has not previously been considered in lizard social systems. Subordinate (smaller) individuals are the recipients of sometimes sustained aggression that can result in tail loss (Riley et al. 2017) and presumably, additional physiological costs such as stress, physical injury and reduced access to food, basking areas and/or refuges. We need to investigate the possibility that early social environment and sibling rivalry may be more common than previously believed. Furthermore, as Stamps (see Stamps 1978; Stamps and Krishnan 1994a, b, 1995) has shown, juvenile aggression among non-kin-based lizard social systems is common and may impact fitness to a greater extent than previously considered. Lizards also demonstrate tremendous diversity in social systems and behavioral repertoires that are used to assert resource-holding potential and social status. Finally, many examples of variation in social systems are associated with polymorphisms in coloration or morphology. Lizards, by virtue of their unique biology, offer a valuable opportunity for enhancing our understanding of the proximate and ultimate function of aggression and its role in social behavior.

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