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How do lizards determine dominance? Applying ranking algorithms to animal social behaviour

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Dominance relationships are a defining feature of the social organization of many animal species. Populations structured by absolute dominance usually maintain a generally linear hierarchy, while relative dominance occurs, for example, within territorial populations where an animal is likely to be dominant within its territory. Because relative dominance is dependent on social context, the traits associated with it are often unclear. Green anole lizards, *Anolis carolinensis*, are an ideal system in which to determine dominance-related traits, as anoles use territorial defence in most natural environments, but establish a dominance hierarchy at high densities such as those that occur in captivity. We hypothesized that anoles use similar morphological and behavioural traits to determine social status under both forms of social organization. To test this, we studied a natural population of anoles to determine the traits most predictive of male territory size and quality (as measured by the number of females overlapping a male's territory). While these measures of territory may be related, they measure different components of territorial success. We then used mathematical ranking algorithms to quantify dominance in a tournament of paired arena trials, and identified traits associated with rank. Our results showed that lizards with wider heads had higher social rank, while those with longer heads were more successful at territorial defence. We also found that, independently of morphology, lizards who behaved more aggressively ranked higher in dominance trials, although behaviour did not predict measures of territory. Together, our results indicate that different traits may determine absolute and relative dominance in the green anole.

Conflicts arise in animal populations when individuals compete for limited resources, such as food, mates or refuges. Physical confrontations between individuals are energetically expensive (Neat, Taylor, & Huntingford, 1998) and potentially dangerous (Clutton-Brock, Albon, Gibson, & Guinness, 1979), so animals of many species use social behaviours to determine resource distribution without frequent fighting. These interactions often involve ritualized displays of size, strength or quality, by which individuals compete to establish social status or dominance over their opponents (Ryan, 1985; Senar, 2006). In populations in which dominance has been established, animals with higher status gain priority access to valuable resources (Kaufmann, 1983) and often experience increased reproductive success (e.g. Schubert et al., 2007; Wroblewski et al., 2009).

Kaufmann (1983) described two broad classifications of dominance: absolute and relative. In populations with absolute dominance, individuals compete to determine their rank in a generally linear hierarchy. Once established, animal interactions are determined by these absolute rankings, regardless of the time or location of future competitions. Even so, strictly linear hierarchies are rare in nature, and most observed hierarchies have some cyclic (i.e. nontransitive) relationships (for example, where A is dominant to B and B is dominant to C, but C is dominant to A; Shizuka & McDonald, 2012). In contrast, in species governed by relative dominance, relationships among individuals predictably change based on when and where competitions occur. Territorial species provide an example of relative dominance, as these animals are more likely to win interactions occurring on their own territories (e.g. Johnsson, Nobbelin, & Bohlin, 1999; Takeuchi & Honda, 2009; Tobias, 1997).

Absolute and relative dominance are often considered to be mutually exclusive (Maher & Lott, 1995), such that a single population may experience only one of the two forms of dominance. For

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example, it is generally assumed that territorial animals only know their social rank in relation to their neighbours, as they do not have direct information on the relative fighting ability of individuals they have not yet encountered (Stamps, 1994). Yet, when natural hierarchies form, it is rare that interactions occur between all pairs of individuals; animals may instead infer their position in an overall hierarchy using feedback from interactions within a subset of the population (Hobson & DeDeo, 2015). Whether a population is structured by absolute or relative dominance, individual animals generally rely on the use of display and/or fighting behaviours to establish social status, and they require pairwise comparisons to determine their relative ranks. In this study, we sought to determine the nature of the relationship between these two modes of social organization. Are they independent, maintained by similar behaviours but favouring different traits? Or are they associated, such that an animal's potential position in a dominance hierarchy (in a laboratory environment) is related to the size and/or quality of its territory (in the field)?

We addressed these questions by examining social behaviour in the green anole lizard, *Anolis carolinensis*. Green anoles have become model organisms in the study of behaviour in the field and laboratory, particularly regarding social and reproductive behaviours (reviewed in Crews & Gans, 1992; Greenberg, 1994, 2003; Greenberg et al., 1989; Jenssen, Lovern, & Congdon, 2001; Lovern, Holmes, & Wade, 2004; Wade, 2012). Green anoles of both sexes, but most commonly males, generally defend territories against same-sex rivals (e.g. Jenssen & Nunez, 1998), and thus they predominantly utilize relative dominance in maintaining social networks. However, in particularly dense populations (e.g. those sustained in captivity), male green anoles will forgo territorial defence and instead establish a dominance hierarchy (reviewed in Alberts, 1994; Stamps, 1977). In both the laboratory and field, anoles use the same series of well-described ritualized displays to defend territories and/or establish dominance (Decourcy & Jenssen, 1994; Greenberg, 1977, 2003; Greenberg & Noble, 1944; Jenssen, 1977; Jenssen, Greenberg, & Hovde, 1995). In brief, most aggressive displays between male green anoles usually begin with both individuals performing a series of dynamic displays including push-ups, headbobs and extension of a throat fan called a dewlap. If the interaction continues to escalate, the lizards may move closer together, aligning their bodies in parallel as they begin to circle one another. Static display modifiers such as the development of eyespots, raising a nuchal crest, dorsolateral compression and changing body colour between green and brown may further signal enhanced aggression. Body colour may also indicate stress (particularly if a lizard has brown or blotchy coloration), which can further influence competitive interactions. (While different components of display behaviours are commonly performed together, both the dynamic displays and the static modifiers may also occur on their own.) Ultimately, in the most aggressive encounters, the lizards may 'lock jaws' and attempt to throw each other off the perch. At any point during an interaction, an individual may cease to display or withdraw from the area, thus conceding dominant status to his opponent.

In addition to these behavioural displays of aggression that may establish or maintain dominance, several morphological traits have been shown to predict territorial success and social rank in anoles. In particular, previous studies have suggested that male anole body size is positively associated with territory size and quality (reviewed in Losos, 2009) and dominance rank (e.g. Tokarz, 1985). Social dominance has also been linked to head size (a trait closely related to bite force; Henningsen & Irschick, 2012; Perry, LeVering, Girard, & Garland, 2004), locomotor ability (Lailvaux, Herrel, VanHooydonck, Meyers, & Irschick, 2004; Perry et al., 2004), dewlap size (Lailvaux et al., 2004; Vanhooydonck, Herrel, Van Damme, & Irschick, 2005) and eyespot development (Larson & Summers, 2001) in laboratory studies of anoles; and tail length is a status symbol in several iguanid lizards (Cooper, 2003; Fox, Heger, & Delay, 1990).

In this study, we sought to determine the morphological and behavioural traits associated with relative (territorial) and absolute (hierarchical) dominance in male green anoles. We used two field measures of territorial success to assess relative dominance: territory size and quality (as determined by the number of females overlapping a male's territory). To quantify absolute dominance, we adapted ranking algorithms developed in the context of sports tournaments to describe the outcomes of a series of paired encounters in a captive population of anoles. Using these measures, we tested the hypothesis that male green anoles use the same combination of these behavioural and morphological traits to determine territory size, territory quality, and social rank. In particular, we predicted that all three measures of social status would be positively related to body size, a trait previously associated with dominance in both laboratory and field settings.

METHODS

Quantifying Territorial Behaviour in a Field Population

Morphological measurements and behavioural observations

We established a 35 × 25 m study plot in Palmetto State Park, Gonzales, Texas, U.S.A. in a seasonal swamp dominated by dwarf palmettos (*Sabal minor*). Between 29 May and 12 June 2013 (i.e. in the middle of the green anole breeding season), we caught 73 adult green anoles (33 males, snout–vent length (SVL) > 55 mm; 40 females, SVL > 45 mm) in the plot by hand or noose. Upon capture, we marked each lizard by sewing a unique bead tag into the tail musculature using surgical wire (Fisher & Muth, 1989). For each male, we also performed a series of morphological measurements. We measured SVL and tail length to the nearest 1 mm, and mass to the nearest 0.1 g. Head length, head width, and dewlap length were all measured to the nearest 0.1 mm using digital callipers, as follows. Head length was measured as the distance from the parietal eye to the tip of the snout, and head width was measured at the widest part of the skull (the anterior base of the cranium). Dewlap length, a proxy for dewlap size (Johnson & Wade, 2010), was measured from the insertion point of the second ceratobranchial cartilage (the cartilage that lines the exterior of the extended dewlap) in the lower jaw to the distal end of the cartilage at the abdomen. After measurements and/or marking were completed, we released the lizard at its site of capture.

After a minimum of 24 h postcapture, we conducted behavioural observations on marked male lizards. Over 3 weeks, we performed 5–30 min focal behavioural observations (average = 24.2 min) on individual males between 0900 and 1700 hours, attempting to observe all lizards across the daily time frame. During observations, we recorded all social behaviours, focusing on the number of dewlap extensions and push-up displays performed. Each lizard was observed for a maximum of 3 h, with multiple observations of an individual lizard separated by at least 2 h. All lizards with a minimum of 2 h of observation, and those that were observed in a minimum of four observations, were included in subsequent analyses.

Territory measurements

To estimate lizard territories, we established reference points throughout the study plot. Each time a marked lizard was sighted, we measured the distance from the lizard's perch to the closest reference point using measuring tape, and the angle from north between the two points to the nearest degree using a compass. In