CURRENT ISSUES – PERSPECTIVES AND REVIEWS

Breaking the Social–Non-social Dichotomy: A Role for Reptiles in Vertebrate Social Behavior Research?

J. Sean Doody*, Gordon M. Burghardt*† & Vladimir Dinets†

* Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA
† Department of Psychology, Austin Peay Building, University of Tennessee, Knoxville, TN, USA

(Invited Review)

Correspondence
J. Sean Doody, Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996-1610, USA.
E-mail: jseandoody@gmail.com

Abstract

Although social behavior in vertebrates spans a continuum from solitary to highly social, taxa are often dichotomized as either 'social' or 'non-social'. We argue that this social dichotomy is overly simplistic, neglects the diversity of vertebrate social systems, impedes our understanding of the evolution of social behavior, and perpetuates the erroneous belief that one group—the reptiles—is primarily 'non-social'. This perspective essay highlights the diversity and complexity of reptile social systems, briefly reviews reasons for their historical neglect in research, and indicates how reptiles can contribute to our understanding of the evolution of vertebrate social behavior. Although a robust review of social behavior across vertebrates is lacking, the repeated evolution of social systems in multiple independent lineages enables investigation of the factors that promote shifts in vertebrate social behavior and the paraphyly of reptiles reinforces the need to understand reptile social behavior.

Social behavior broadly refers to any interaction between two or more members of the same species (Allaby 2009). Virtually all individual animals will interact with conspecifics at some stage of their lives; therefore, it should be expected that each species will possess some inherent capacity for social interaction. The study of social behavior in vertebrates has highlighted extensive variation among species in both the complexity and frequency of social interactions, with each species positioned somewhere along the spectrum between predominately solitary and highly social (Tinbergen 1953; Alexander 1974). Such a univariate spectrum ignores the many different modes of social organization and sociality found among animals. Are polygamous species more social than monogamous ones, dominance hierarchies more social than territoriality, large herding species more social than their group hunting predators? Simple metrics are hard to apply across disparate taxa.

Regardless, birds, mammals, and to a lesser extent fishes are widely recognized as the most social vertebrate lineages due to the widespread incidence of large, stable aggregations, the complexity of the interactions within these social groupings, the prevalence of prolonged parental care of neonates, and the high level of social deception in some groups (Tinbergen 1953; Wilson 1975; Bennett & Owens 2002; Krause & Ruxton 2002). Similarly, amphibians are renowned for having complex acoustic communication systems and social systems that involve breeding aggregations, parental care, and pair bonds (Heatwole & Sullivan 1995). In contrast, reptiles are often stereotyped as solitary and aggressive, lacking parental care or stable social aggregations, with little diversity to their social behavior beyond territoriality and dominance hierarchies (Wilson 1975; MacLean 1990; Wilkinson et al. 2010a). This perspective has dominated, despite the view by some ethologists that reptiles have an important role in social behavior research (Brattstrom 1974; Burghardt 1977; Carpenter & Ferguson 1977; Fox et al. 2003).

The documented prevalence of different kinds of social behavior and social interactions does differ among vertebrate lineages. For example, the proportion of species that provide parental care to their eggs or young is highest in mammals and birds and is lower in fishes, amphibians, and reptiles (Fig. 1). Despite this pattern and the fact that each vertebrate group includes species that have varying levels of sociality
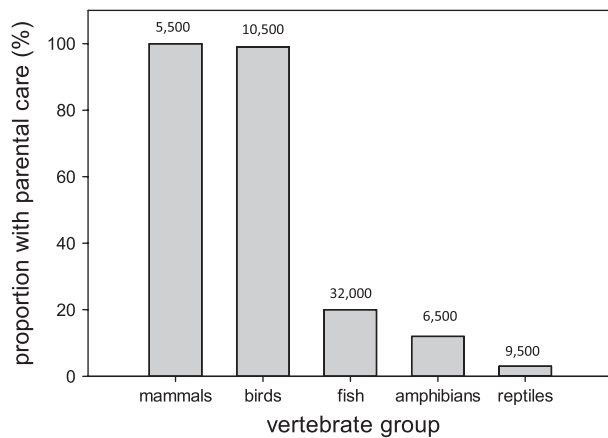
Fig. 1: Relative occurrence of parental care (after birth or hatching) across vertebrates. Numbers above bars indicate approximate species richness for that group.

and parental care, researchers have often dichotomized social behavior in vertebrates by labeling species as either 'social' or 'non-social' (Sharp et al. 2005; Belleman & Swenson 2006; Honer et al. 2007), with reptiles regularly labeled as 'non-social' (Wilkinson et al. 2010a; Wilkinson & Huber 2012). We contend that this social dichotomy is simplistic, scientifically misleading, neglects the diversity of social systems that is evident within genera, families, and vertebrate classes, and thus impedes our understanding of social behavior in reptiles and its evolution across vertebrates. For example, spatial and temporal variation in the social organization of several vertebrate species (Layhausen 1965; Lott 1991) presents challenges when assigning species to particular categories. Conversely, regarding reptiles as 'non-social' ignores their diverse and often complex social behaviors. This perspective ultimately results in reptiles being overlooked by researchers examining vertebrate social behavior, limits the scope of the reptile social behavior studies, and creates the impression that reptile species provide little opportunity for studying the mechanisms underlying the evolution of complex social behavior. In reality, the types and extent of sociality differ within all of the classes of vertebrates, including reptiles. The effects of this dismissal of reptiles as having complex social behavior, emotions, and even play have been ensconced in the literature by leading neuroscientists based on brain structures (e.g., MacLean 1985, 1990). However, recent comparative neuroscience is documenting the ancient evolutionary origins of neural structures underlying complex social behavior (e.g. Bass & Chagnaud 2012).

We contend that (1) 'social' and 'non-social' should be used to describe behaviors or contexts, rather than taxa, and (2) the diversity and complexity of social behavior in reptiles have been underestimated (Doody 2011; Clark et al. 2012). Here, we (1) briefly address researchers' apparent neglect of social behavior in reptiles and (2) highlight the impressive diversity and complexity of social systems that exist in reptiles, within the broader vertebrate context. We, thus, want to bring to a wider audience some of the remarkable (and not always recent) findings that indicate how reptiles can contribute to our understanding of the evolution of social behavior in vertebrates. In this brief review, we consider the paraphyletic group of non-avian reptiles and hope that it will prompt an exhaustive review of social behavior that incorporates the monophyletic reptiles + birds clade when analyzing the evolution of social behavior across all vertebrates.

How and why has Reptile Social behavior been Neglected?

Research effort is not evenly distributed among the vertebrate groups, with reptiles receiving far less attention compared to birds, mammals, and fishes (Gaston & May 1992; Bonnet et al. 2002; Pawar 2003). For example, a survey of 1,000 scientific articles revealed that although species richness is greater in reptiles than in mammals, the behavioral literature contains four times as many articles on mammals (Bonnet et al. 2002). There is also a particularly strong bias toward birds (44% of all journal articles on vertebrates) despite birds representing only 20% of the world's vertebrate diversity (Bonnet et al. 2002). The neglect of reptile social behavior may simply be a consequence of the broader bias against research on reptiles, but the appearance, life history, ecology, or behavior of reptiles might also contribute (Kellert 1993; Pawar 2003). Humans exhibit less affinity with 'scaly' reptiles compared to 'cute and cuddly' birds and mammals, and many people fear and actively avoid reptiles, especially snakes and crocodilians (e.g., Kellert 1993). Reptiles lack the facial expressions used by many mammals, and do not use vocal signals as often as birds do. Squamate reptiles, in particular, communicate using chemosensory cues that are not detectable by the human senses (Burghardt 1970; Pianka & Vitt 2003). This may lead researchers to focus on vertebrate groups (e.g., birds, mammals, and amphibians) whose communication systems (e.g., visual, auditory) are more salient to human sensory perceptions (see a discussion of this bias in Rivas & Burghardt 2002).

The reproductive behavior of birds and mammals is generally more conspicuous compared to that of non-avian reptiles, and this has consequences for the relative contribution of vertebrate groups to theory in behavioral ecology. Highlighting the disparity in the extent of our knowledge of the breeding behavior of birds and reptiles is the existence of quite complete field guides to the identification of birds' eggs and nests from at least three continents, yet we do not even know where most reptiles lay their eggs and thus how many lay communally (reviewed in Doody et al. 2009). In an illuminating example, the proportion of Australian lizards known to nest communally rises from 0.06 to 0.86 when species for which nests have not been discovered are excluded (Doody et al. 2009), suggesting that communal breeding (and possibly other social behaviors) has been vastly underestimated in reptiles due to the inconspicuousness of their nests. The perceived absence of such social behaviors in reptiles may generate a feedback loop that acts to perpetuate the bias toward studying social behavior in birds, mammals, and fishes, rather than in reptiles.

There are several additional obstacles that may inhibit the completion and publication of studies on reptile social behavior. For instance, it is often more difficult to obtain funding for reptile research compared to studies on birds and mammals (Czech et al. 1998). In addition, 'taxonomic chauvinism' may occur among referees for scientific journals and presumably also the referees for funding bodies, which leads to reptile researchers using more space in the introduction of their articles 'justifying' how their study makes a contribution to the field (Bonnet et al. 2002). As a consequence, the majority of studies on reptile social behavior are published in taxon-specific journals (e.g., herpetology journals) rather than broader journals in the fields of behavioral ecology and evolutionary biology. Perhaps relatedly, texts on animal behavior, behavioral ecology, the evolution of behavior, comparative cognition and the like largely ignore the scientific literature on reptiles. Thus, we believe that many behavioral researchers are unaware of the complexity and diversity of social systems in reptiles (Lott 1991) and of the opportunities that reptiles provide for examining evolutionary hypotheses in vertebrate social behavior (While et al. 2009a; Davis et al. 2011).

Social behavior in Reptiles

In 1977, a handful of researchers held the first ever symposium on the social behavior in reptiles, at the 64th annual meeting of the American Society of Zoologists, now the Society for Integrative and Comparative Biology (Greenberg & Crews 1977). Surprisingly, after more than three decades, there remains no detailed review of social behavior in reptiles or in vertebrates more generally. Herein, we highlight social behavior in reptiles, emphasizing a recent surge in the number of studies of reptilian social behavior.

Somewhat remarkably, social behavior can start in the egg. A recent symposium on 'environmentally cued hatching in animals' revealed a diversity of social interactions not only between embryos and parents, but also between embryos within a clutch (Doody 2011; Spencer & Janzen 2011; Warkentin 2011). For example, recent experiments demonstrated that some turtle embryos can use sibling vibrations as a cue to expedite hatching and increase survival during imminent nest flooding (Doody et al. 2012). In another example, turtle embryos positioned deeper in subterranean nests develop slower than their clutchmates due to thermal gradients, but at least two species can 'catch up' and achieve synchronous hatching by increasing heart rate or metabolic rate (McGlashan et al. 2011; Spencer & Janzen 2011). The vocalizations of crocodilian embryos fine-tune hatching synchrony and also stimulate mothers to open the nest to free hatchlings and carry them to water (Vergne et al. 2009). Similarly, hatching-competent turtle embryos of at least one species vocalize (Ferrara et al. in press). Although mothers do not excavate hatchlings, a social function is likely; juveniles and adults also vocalize underwater (Ferrara et al. in press). Collectively, these social behaviors facilitate adaptive shifts in timing of hatching and parallel the complexity found in oviparous fish, amphibians, and birds (Warkentin & Caldwell 2009; Warkentin 2011).

Parental care in reptiles is less common and usually less complex, with the exception of crocodilians, than in other vertebrates. For example, around 97% of all reptile species abandon their eggs soon after laying (Fig. 1), although egg attendance ranges from days to weeks in tuataras and some iguanas and to the entire incubation period in other lizards, snakes, and crocodilians (Shine 1988; Somma 2003; Whitaker 2007). It should be noted, however, that parental care may occur in turtles (Ferrara et al. in press) and that until recently, it was claimed that no snakes had postnatal parental care (Clark et al. 2012). On the other hand, all crocodilians have some parental care. Cooperative breeding, which is common in birds, mammals, and fish (Solomon & French 1996; Stacey & Koenig 1990; Wong & Balshine 2011), is not yet documented in reptiles. However, female broad-snouted caimans take

turns guarding multi-parental crèches (Pinheiro 1996). This advanced form of cooperative offspring care might eventually be found in other crocodilians as well, because juveniles of other caiman and alligator species frequently form multi-parental crèches, which are protected by more than one female (Vladimir Dinets pers. obs., J. Thorbjarnarson pers. comm.). More generally, crocodilians display a remarkable cascade of maternal care behavior for their eggs and hatchlings, including vocal communication, excavation, carrying hatchlings and eggs to water from the nest, breaking of the eggshell to facilitate hatching, and feeding and protection of the crèche (Pooley 1977; Magnussen 1980; Whitaker 2007; Verne et al. 2009; Brueggen 2010). Biparental care, which is the norm in birds, canids, cichlids, a few amphibian lineages, and some other vertebrates, has only recently been demonstrated in crocodilians (Whitaker 2007; Brueggen 2010). In squamates, parental care is maternal and generally restricted to the egg stage (but see Clark et al. 2012), but there is considerable variation across groups (Fig. 2), and a diversity of strategies exists, including brooding, attendance, guarding, and direct care (Shine 1988; Somma 2003).

Most reptiles are highly precocial to independent upon birth or hatching, often dispersing and setting up home ranges as juveniles, and this may have profound consequences for their cognitive abilities by removing the period of protected juvenile life (Burghardt, 1988). However, desert skinks cooperatively construct a long-term home for family members (McAlpin et al. 2011). Without parental protection, hatchling iguanas engage in group vigilance when emerging from the nest (Burghardt 1977; Burghardt

et al. 1977). Conspicuous territoriality is evident in the signaling, posturing and combat between males of snakes, lizards, turtles, and crocodilians defending access to mates and other resources, and in large animals like crocodiles and king cobras guarding their nests (Shine 1988, 1989). Large, stable social groups are widespread among lizards (Gardner et al. 2001; Chapple 2003; Davis et al. 2011). Social behavior in the lizard genus *Egernia* includes kin-based social groups, kin recognition, inbreeding avoidance mechanisms, parental care, group antipredator behaviors, and long-term social and genetic monogamy of up to 20 yr (Lanham & Bull 2004; Bull 2000; Cahan et al. 2002; Gardner et al. 2002; Stow & Sunnucks 2004; O'Connor & Shine 2006; Sinn et al. 2008). Such social systems are currently known in less than 1% of lizard species (Davis et al. 2011), but this is almost certainly an underestimation because intensive research using molecular techniques has only commenced during the last decade, and the taxonomic breadth of the research has been limited. Social group structure in lizards can vary within and among species (e.g., While et al. 2009b), with the presence of social aggregations in populations or species being affected by both life history (e.g., viviparity, delayed dispersal, longevity; Davis et al. 2011) and ecological (e.g., habitat limitation; Michael et al. 2010) factors (Chapple 2003). Even in snakes, considered the least social of reptiles, aggregations based on social cues (Burghardt 1977) and social recognition based on prior competitive encounters occur (Yeager & Burghardt 1991), and recent research demonstrated that pregnant females and juveniles preferentially aggregate with kin (Clark et al. 2012).

The advanced behavior of cooperative hunting may be common in crocodilians and sea snakes, where it receives regular attention from documentary film crews, but remains mostly undescribed (but see Dinets 2010). Rare observations indicate that cooperative hunting by at least four crocodilian species sometimes involves role partitioning (Mikloukho-Maklay 1892; Vladimir Dinets unpubl. data). Such partitioning is extremely rare in vertebrates (Gazda et al. 2005), known from only a few mammal and bird species and two species of fish (Bednarz 1988; Leonardi 1999; Bowman 2003; Gazda et al. 2005; Bshary et al. 2006; Yosef & Yosef 2010).

Courtship and mating are difficult to observe in nature, but the advent of molecular ecology has largely removed this impediment for determining patterns in mating systems (Sugg et al. 1996; Uller & Olsson 2008). The mating systems of reptiles are complex, including a high level of polygyny and polyandry, but
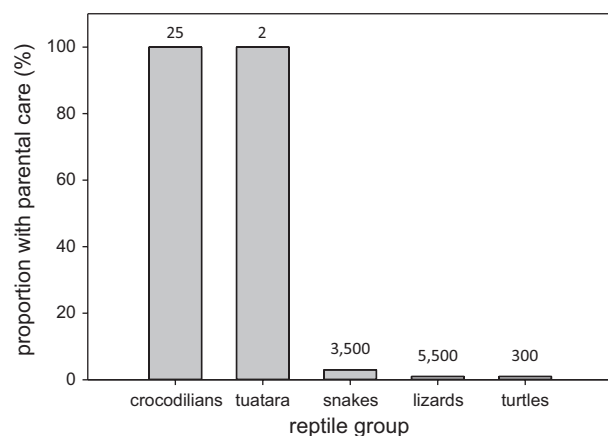

Fig. 2: Relative occurrence of parental care (after birth or hatching) across reptiles. Numbers above bars indicate approximate species richness for that group.

monogamy and parthenogenesis also occur (Bull 2000; Rivas & Burghardt 2005; Uller and Olsson 2008; Lance et al. 2009; Booth et al. 2011). Only recently, has it become clear that alternative mating strategies occur in virtually all animal lineages (Zamudio & Sinervo 2003). The culprit here for reptiles is probably their cryptic behavior, but in some cases, the secretive nature of reptiles cannot explain our lack of understanding of courtship behavior (see Rivas & Burghardt 2005). For example, the American Alligator, the largest non-marine predator in North America, is arguably the world's most studied reptile (Brisbin et al. 1986). However, one of the most striking features of its natural history, the courtship 'dances' involving up to a hundred animals, has only recently been described (Dinets 2010), even though this remarkable spectacle is routinely observed by tourists in the Florida Everglades. Other mating behaviors such as male mate guarding have been documented in some lizards and may be much more common than we realize (Hasegawa 2003). Revealing reptilian courtship behaviors can spawn research that significantly advances our understanding of social behavior and its evolution in vertebrates. For example, recent research quantifying mating success in lekking marine iguanas revealed that the strong male mating skew was variable among individuals across years, and thus, head-bobbing behavior in any year did not indicate good genes (Vitousek et al. 2008).

Reptile signaling, an essential part of social behavior, is receiving renewed attention. Perhaps, most exciting is the discovery that at least two species of unrelated turtles can vocalize underwater (Giles et al. 2009; Ferrara et al. in press). The complex multimodal long-distance signaling systems of crocodilians, first described in the late 1970s (Garrick & Lang 1977; Garrick et al. 1978), have been virtually ignored for almost 30 yr, with just a handful of studies (Vliet 1989). Only very recently, has there been some renewal of research interest, with the first overview of long-distance signaling in extant crocodilians finally completed (Dinets 2011). Non-signals can also be recognized by conspecifics; recent experiments with tortoises demonstrated for the first time that reptiles are able to follow the gaze of conspecifics (Wilkinson et al. 2010b) as well as possible predators (Burghardt & Greene 1988). Play, including social play, considered non-existent in reptiles till recently (e.g., MacLean 1985, 1990) has been documented in turtles, lizards, and crocodilians (Kramer & Burghardt 1998; Burghardt 2005).

Underlying much of the above social behavior is one of the most important conceptual advances in biological research in the last 25 yr: conspecific attraction (Stamps 1988). Conspecific attraction, a little known concept in the 1980s, paved the way for modern behavioral research to reveal the complexities of animal interactions and how those interactions affect decisions, other biological phenomena, and fitness (e.g., Allee effect). The demonstration of conspecific attraction in reptiles has generally lagged behind that in other taxa (but see Burghardt 1977; 1983; Stamps 1987) but considerable laboratory and field data are now available that are changing our underlying view of reptile social aggregations from 'artifacts of a common physical resource' to one that is based on conspecific attraction that provides mutual benefits (for examples see Doody et al. 2009; Clark et al. 2012).

A novel finding of social behavior in reptiles brings home our main point about the misleading nature of repeated uses of the non-social label. Researchers recently demonstrated social learning in a 'non-social' tortoise (Wilkinson et al. 2010a) and concluded that their finding overturns the current evolutionary paradigm that 'social living' *preceded* social learning (Honer et al. 2007; Wilkinson & Huber 2012). However, their 'non-social' label for tortoises is based on limited field observations, and evidence for social behavior in turtles is now rapidly accumulating (Wendland et al. 2010; Wilkinson et al. 2010b; Davis & Burghardt 2011; Doody et al. 2011). In particular, Davis & Burghardt (2011) recently demonstrated social learning in an aquatic turtle that often lives alongside conspecifics. Thus, the findings of Wilkinson et al. (2010a) actually *support* the idea that tortoises can be social, undermining their claim of a paradigm shift in the evolution of social learning. As their mistake has received considerable publicity, we think that the authors' misinterpretation of their species as 'non-social', accepted uncritically, would confuse and impede our understanding of both the evolution of social learning in animals and of the social behavior repertoire of tortoises.

Conclusions and Future Directions

The apparent neglect of reptilian social behavior by researchers has recently been offset by a surge in studies using reptiles as subjects. But, is more research attention to social behavior in reptiles really needed and, if so, why? First, the social repertoire of reptiles is diverse, and fresh perspectives and methodological advances are increasingly facilitating paradigm-shifting discoveries in these secretive animals. Second, there have been multiple independent origins of social behavior within vertebrates, and numerous

transitions or shifts along the social continuum (e.g., solitary → social or social → solitary) within taxonomic groups (Cahan et al. 2002). Thus, reptilian groups offer opportunities to test putative factors in independent radiations. Concentrating research effort on particular taxonomic groups may limit or bias our understanding of vertebrate social behavior, while studying social behavior in lineages that differ in key aspects of their biology is likely to enhance our knowledge of the factors that drive the origin and persistence of social behavior. Despite their often secretive nature, reptiles also hold advantages for the study of social behavior, such as their low vagility and thus high site fidelity relative to other vertebrates (Fox et al. 2003; Clark et al. 2012). The often-large clutch and litter sizes, along with limited parental care, make genetic and common garden experiments potentially more powerful. Some groups such as diurnal lizards occupy small conspicuous territories and are indifferent to human observers (Fox et al. 2003), which is rare with small mammals or those with large home ranges. Thus, combining studies of conspicuous species with innovative approaches for detecting social behavior in secretive species will contribute to our understanding of social behavior in vertebrates. A rigorous review of social behavior is still lacking, both among reptiles and among vertebrates in general. Including reptiles in such reviews should generate insights into the evolutionary drivers of social behavior, provided that a continuum approach is used, rather than a dichotomous framework.

Acknowledgements

Literature Cited

Alexander, R. D. 1974: The evolution of social behavior. Annu. Rev. Ecol. Syst. **5**, 325—383.

Allaby, M. 2009: A dictionary of Zoology, 3rd edn. Oxford University Press, Oxford.

Bass, A. H. & Chagnaud, B. P. 2012: Shared developmental and evolutionary origins for neural basis of vocal–acoustic and pectoral–gestural signaling. PNAS **109**, 10677—10684. (in press).

Bednarz, J. C. 1988: Cooperative hunting in Harris' Hawks (*Parabuteo unicinctus*). Science **39**, 525—1527.

Belleman, E. & Swenson, J. E. 2006: Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology **112**, 238—246.

Bennett, P. M. & Owens, I. P. F. 2002: Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction. Oxford University Press, Oxford.

Bonnet, X., Shine, R. & Lourdais, O. 2002: Taxonomic chauvinism. Trends Ecol. Evol. **17**, 1—3.

Booth, W., Million, L., Reynolds, R. G., Burghardt, G. M., Vargo, E. L., Schal, C., Tzika, T. & Schuett, G. W. 2011: Consecutive virgin births in the New World boid snake, the Columbian rainbow boa, *Epicrates maurus*. J. Hered. **102**, 759—763.

Bowman, R. 2003: Apparent Cooperative Hunting in Florida Scrub-Jays. Wilson Bull. **115**, 197—199.

Brattstrom, B. H. 1974: The evolution of Reptilian social behavior. Amer. Zool. **14**, 35—49.

Brisbin, I. L., Ross, C. A., Downes, M. C., Staton, M. A. & Gammon, B. 1986: A Bibliography of the American Alligator. Savannah River National Environmental Research Park, Savannah.

Brueggen, J. 2010: Crocodilians: fact vs. fiction. In: Crocodiles. Proceedings of the 16th working meeting of the Crocodile Specialist Group of the Species Survival Commission of IUCN – World Conservation Union convened in Gainesville, Florida, 7–10 October 2010, pp. 204—211.

Bshary, R., Hohner, A., Ait-el-Djoudi, K. & Fricke, H. 2006: Interspecific Communicative and Coordinated Hunting between Groupers and Giant Moray Eels in the Red Sea. PLoS Biol. **4**, e431.

Bull, C. M. 2000: Monogamy in lizards. Behav. Process. **51**, 7—20.

Burghardt, G. M. 1970. Chemical perception in reptiles. In: Communication by Chemical Signals. (Johnston, J. W. Jr, Moulton, D. G. & Turk, A., eds). Appleton-Century-Crofts, New York, pp. 241—308.

Burghardt, G. M. 1977: Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. Amer. Zool. **17**, 177—190.

Burghardt, G. M. 1988: Precocity, play, and the endotherm-ectotherm transition: profound reorganization or superficial adaptation? In: Handbook of Behavioral Neurobiology. Vol. 9. Developmental Psychobiology and Behavioral Ecology (Ed. by E. M. Blass), pp. 107—148 New York: Plenum Press.

Burghardt, G. M. 2005: The Genesis of Animal Play: Testing the Limits. MIT Press, Cambridge.

Burghardt, G. M. & Greene, H. W. 1988: Predator simulation and duration of death feigning in neonate hognose snakes. Anim. Behav. **36**, 1842—1844.

Burghardt, G. M., Greene, H. W. & Rand, A. S. 1977: Social behavior in hatchling green iguanas: life at a reptile rookery. Science **195**, 689—691.

Cahan, S. H., Blumstein, D. T., Sundstrom, L., Liebig, J. & Griffin, A. 2002: Social trajectories and the evolution of social behavior. Oikos **96**, 206—216.

Carpenter, C. C. & Ferguson, G. W. 1977. Variation and evolution of stereotyped behavior in reptiles. In: Biology

of the R eptilia, Vol. 7A (Gans, C. & Tinkle, D. W., eds). Academic Press, New York, pp. 335—554.

Chapple, D. G. 2003: Ecology, life-history and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. Herpetol. Monogr. **17**, 145—180.

Clark, R. W., Brown, W. S., Stechert, R. & Greene, H. W. 2012: Cryptic sociality in rattlesnakes (*Crotalus horridus*) detected by kinship analysis. Biol. Lett. **8**, 523—525.

Czech, B., Krausman, P. R. & Borkhataria, R. 1998: Social construction, political power, and the allocation of benefits to endangered species. Conserv. Biol. **12**, 1103—1112.

Davis, K. M. & Burghardt, G. M. 2011: Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. J. Comp. Psychol. **125**, 404—410.

Davis, A. R., Corl, A., Surget-Groba, Y. & Sinervo, B. 2011: Convergent evolution of kin-based sociality in a lizard. Proc. Roy. Soc. Lond. B **278**, 1507—1514.

Dinets, V. 2010: Nocturnal behavior of American alligator (*Alligator mississippiensis*) in the wild during the mating season. Herp. Bull. **111**, 4—11.

Dinets, V. 2011: The Role of Habitat in Crocodilian Communication. Doct. Diss., University of Miami, Florida, USA.

Doody, J. S. 2011: Environmentally-cued hatching in reptiles. Integr. Comp. Biol. **51**, 49—61.

Doody, J. S., Freedberg, S. & Keogh, J. S. 2009: Communal egg-laying in reptiles and amphibians: evolutionary patterns and hypotheses. Q. Rev. Biol. **84**, 229—252.

Doody, J. S., Castellano, C. M., Rakotondrainy, R., Ronto, W. M., Rakotondriamanga, T. M., Duchene, J. J. & Randria, Z. 2011: Aggregated Drinking Behavior of Radiated Tortoise*s (Astrochelys radiata)* in Arid Southwestern Madagascar. Chelonian Conserv. Biol. **10**, 145—146.

Doody, J. S., Stewart, B., Camacho, C. & Christian, K. 2012: Good vibrations? Sibling embryos expedite hatching in a turtle Anim. Behav. **83**, 645—651.

Ferrara, C. R., Vogt, R. C. & Sousa-Lima, R. S. in press: Turtle vocalizations as the first evidence of post-hatching parental care in Chelonians. J. Comp. Psychol., in press.

Fox, S. F., McCoy, K. & Baird, T. A. 2003: Lizard Social Behavior. John Hopkins University Press, Baltimore.

Gardner, M. G., Bull, C. M., Cooper, S. J. B. & Duffield, G. A. 2001: Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. Mol. Ecol. **10**, 175—183.

Garrick, L. D. & Lang, J. W. 1977: Social signals and behaviors of adult alligators and crocodiles. Am. Zool. **17**, 225—239.

Garrick, L. D., Lang, J. W. & Herzog, H. A. Jr 1978: Social signals of adult American alligators. Bull. Am. Mus. Nat. Hist. **160**, 153—192.

Gaston, K. J. & May, R. M. 1992: Taxonomy of taxonomists. Nature **356**, 281—282.

Gazda, S. K., Connor, R. C., Edgar, R. K. & Cox, F. 2005: A division of labour with role specialisation in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. Proc. Roy. Soc. Lond., B, Biol. Sci. **272**, 135—140.

Giles, J. C., Davis, J. A., McCauley, R. D. & Kuchling, G. 2009: Voice of the turtle: the underwater acoustic repertoire of the long-necked freshwater turtle, *Chelodina oblonga*. J. Acoust. Soc. Am. **126**, 434—443.

Greenberg, N. & Crews, D. 1977: Introduction to the symposium: social behavior in reptiles. Amer. Zool. **17**, 153—154.

Hasegawa, M. 2003: Intraspecific variation in sexual dimorphism and mating system in relation to interisland differences in predation pressure. In: Lizard Social Behavior (Fox, S. F., McCoy, K. & Baird, T. A., eds). John Hopkins University Press, Baltimore, pp. 172—189.

Heatwole, H. & Sullivan, H. 1995: Amphibian Biology, Volume 2: Social Behaviour. Surrey Beatty & Sons, Chipping Norton, Australia.

Honer, O. P., Wachter, P., East, M. L., Sterich, W. J., Wilhelm, K., Burke, T. & Hofer, H. 2007: Female mate-choice drives the evolution of male-biased dispersal in a social mammal. Nature **448**, 798—801.

Kellert, S. R. 1993: The biological basis for human values of nature. In: The Biophilia Hypothesis (Kellert, S. R. & Wilson, E. O., eds). Island Press, Washington, D. C., pp. 42—69.

Kramer, M. & Burghardt, G. M. 1998: Precocious courtship and play in emydid turtles. Ethology, **104**, 38—56.

Krause, J. & Ruxton, G. D. 2002: Living in Groups. Oxford University Press, Oxford.

Lance, S. L., Tuberville, T. D., Dueck, L., Holz-Schietinger, C., Trosclair, P. L. III, Elsey, R. M. & Glenn, T. C. 2009: Multiyear multiple paternity and mate fidelity in the American alligator, *Alligator mississippiensis*. Mol. Ecol. **18**, 4508—4520.

Lanham, E. J. & Bull, C. M. 2004: Enhanced vigilance in groups in *Egernia stokesii*, a lizard with stable social aggregations. J. Zool. **263**, 95—99.

Leonardi, G. 1999: Cooperative hunting of the Jackdaws by the Lanner Falcon (*Falco biarmicus*). J. Raptor Res. **33**, 123—137.

Leyhausen, P. 1965: The communal organisation of solitary mammals. Symp. Zool. Soc. London, **14**, 249—263.

Lott, D. F. 1991: Intraspecific Variation in the Social Systems of Wild Vertebrates. Cambridge University Press, Cambridge.

MacLean, P. 1985: Brain evolution relating to family, play and the separation call. Arch. Gen. Psychiatry, **42**, 405—417.

MacLean, P. 1990: The Triune Brain in Evolution. Plenum, New York.

Magnussen, W. E. 1980: Hatching and crèche formation by *Crocodylus porosus*. Copeia **1980**, 359—362.

McAlpin, S., Duckett, P. & Stow, A. 2011: Lizards cooperatively tunnel to construct a long-term home for family members. PLoS ONE **6**, e19041.

McGlashan, J. K., Spencer, R.-J. & Old, J. M. 2011: Embryonic communication in the nest: metabolic responses of reptilian embryos to developmental rates of siblings. Proc. Roy. Soc. B **279**, 1709—1715. (doi:10.1098/rspb.2011.2074).

Michael, D. R., Cunningham, R. B. & Lindenmayer, D. B. 2010: The social elite: habitat heterogeneity, complexity and quality in granite inselbergs influence patterns of aggregation in *Egernia striolata* (Lygosominae: Scincidae). Austral Ecol. **35**, 862—870.

Mikloukho-Maklay, N. N. 1892: Puteshestviya na Bereg Maklaya [Travels to Maklay Coast]. Russian Academy of Sciences, Saint-Petersburg, pp. 316.

O'Connor, D. & Shine, R. 2006: Kin discrimination in the social lizard *Egernia saxatilis* (Scincidae). Behav. Ecol. **17**, 206—211.

Pawar, S. 2003: Taxonomic chauvinism and the methodological challenged. Bioscience **53**, 861—864.

Pianka, E. R. & Vitt, L. J. 2003: Lizards: Windows to the Evolution of Diversity. University of California Press, Berkeley.

Pinheiro, M. S. 1996: Crescimento de filhotes de jacare-do-papo-amarelo, *Caiman latirostris* (Daudin, 1802), alimentados com fontes proteicas de origem animal. Thesis, Escola Superior de Agricultura Luiz de Queiroz, Piracicaba, San Paulo, Brazil.

Pooley, A. C. 1977: Nest opening response of the Nile Crocodile *Crocodylus niloticus*. J. Zool. **182**, 17—26.

Rivas, J. A. & Burghardt, G. M. 2002: Crotalomorphism: A metaphor to understand anthropomorphism by omission. In: The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition (Bekoff, M., Colin, A. & Burghardt, G. M., eds). MIT Press, Cambridge, MA, pp. 9—17.

Rivas, J. A. & Burghardt, G. M. 2005: Snake mating systems: The revisionary implications of recent findings. J. Comp. Psychol. **119**, 447—454.

Sharp, S. P., McGowan, A., Wood, M. J. & Hatchwell, B. J. 2005: Learned kin recognition cues in a social bird. Nature **434**, 1127—1130.

Shine, R. 1988: Parental care in reptiles. In: Biology of the Reptilia, Vol. 16. Ecology B. Defense and life history. (Gans, C. & Huey, R. B., eds) Alan R. Liss, New York, pp. 275—330.

Shine, R. 1989: Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. **64**, 419—461.

Sinn, D. L., While, G. M. & Wapstra, E. 2008: Maternal care in a social lizard: links between female aggression and offspring fitness. Anim. Behav. **76**, 1249—1257.

Solomon, N. G. & French, J. A. 1996: Cooperative Breeding in Mammals. Cambridge University Press, Cambridge.

Somma, L. A. 2003: Parental behavior in Lepidosaurian and Testudinian Reptiles. Krieger Publishing, Florida.

Spencer, R.-J. & Janzen, F. J. 2011: Hatching behavior in turtles. Integr. Comp. Biol. **51**, 100—110.

Stacey, P. B. & Koenig, W. D. 1990: Cooperative Breeding in Birds. Cambridge University Press, Cambridge.

Stamps, J. A. 1987: Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. Am. Nat. **129**, 629—642.

Stamps, J. A. 1988: Conspecific attraction and aggregation in territorial species. Am. Nat. **131**, 329—347.

Stow, A. J. & Sunnucks, P. 2004: Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. Mol. Ecol. **13**, 443—447.

Sugg, D. W., Chesser, R. K., Dobson, F. S. & Hoogland, J. L. 1996: Population genetics meets behavioral ecology. Trends Ecol. Evol. **11**, 338—342.

Tinbergen, N. 1953: Social behaviour in Animals: with Special Reference to Vertebrates. Methuen, London, UK.

Uller, T. & Olsson, M. 2008: Multiple paternity in reptiles: patterns and processes. Mol. Ecol. **17**, 2566—2580.

Vergne, A. L., Pritz, M. B. & Mathevon, N. 2009: Acoustic communication in crocodilians: from behaviour to brain. Biol. Rev. **84**, 391—411.

Vitousek, M. N., Rubenstein, D. R., Nelson, K. N. & Wikelski, M. 2008: Are hotshots always hot? A longitudinal study of hormones, behavior, and reproductive success in male marine iguanas. Gen. Comp. Endocrinol. **157**, 227—232.

Vliet, K. A. 1989: Social displays of the American alligator. Am. Zool. **29**, 1019—1031.

Warkentin, K. M. 2011: Environmentally cued hatching across taxa: embryos respond to risk and opportunity. Integr. Comp. Biol. **51**, 14—25.

Warkentin, K. M. & Caldwell, l. M. S. 2009: Assessing risk: embryos, information, and escape hatching. In: Cognitive ecology II. The Evolutionary Ecology of Learning, Memory, and Information Use (Dukas, R. & Ratcliffe, J., eds). University of Chicago Press, Chicago, pp. 177—200.

Wendland, L. D., Wooding, J., White, C. L., Demcovitz, D., Littell, R., Berish, J. D., Ozgul, A., Oli, M. K., Klein, P. A., Christman, M. C. & Brown, M. B. 2010: Social behavior drives the dynamics of respiratory disease on threatened tortoises. Ecology **91**, 1257—1262.

While, G. M., Uller, T. & Wapstra, E. 2009a: Family conflict and the evolution of sociality in reptiles. Behav. Ecol. **20**, 245—250.

While, G. M., Uller, T. & Wapstra, E. 2009b: Within-population variation in social strategies characterise the social and mating system of an Australian lizard, *Egernia whitii*. Austral Ecol. **34**, 938—949.

Whitaker, N. 2007: Extended parental care in the Siamese crocodile *Crocodylus siamensis* (Schneider). Russian J. Herp. **14**, 1—4.

Wilkinson, A. & Huber, L. 2012. Cold-blooded cognition: reptilian cognitive abilities. In: The Oxford Handbook of Comparative Evolutionary Psychology (Vonk, J. & Shackelford, T. K., eds). Oxford University Press, Oxford, pp. 129—143.

Wilkinson, A., Kuenstner, K., Mueller, J. & Huber, L. 2010a: Social learning in a non-social reptile (*Geochelone carbonaria*). Biol. Lett. **6**, 614—616.

Wilkinson, A., Mandl, I., Bugnyar, T. & Huber, L. 2010b: Gaze following in the red-footed tortoise (*Geochelone carbonaria*). Anim. Cogn. **13**, 765—769.

Wilson, E. O. 1975: Sociobiology: the New Synthesis. Belknap Press of Harvard, Cambridge, MA.

Wong, M. & Balshine, S. 2011: The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. Biol. Rev. **86**, 511—530.

Yeager, C. & Burghardt, G. M. 1991: The effect of food competition on aggregation: evidence for social recognition in the plains garter snake (*Thamnophis radix*). J. Comp. Psychol. **105**, 380—386.

Yosef, R. & Yosef, N. 2010: Cooperative hunting in Brown-Necked Raven (*Corvus rufficollis*) on Egyptian Mastigure (*Uromastyx aegyptius*). Ethology **28**, 385—388.

Zamudio, K. R. & Sinervo, B. 2003: Ecological and social contexts for the evolution of alternative mating strategies. In: Lizard Social Behavior (Fox, S. F., McCoy, J. K. & Baird, T. A., eds). Johns Hopkins University Press, Baltimore, pp. 83—106.